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Evolution of *Megacricetodon* from the Aragonian and Vallesian (Miocene) of the Iberian Peninsula

Evolución del género Megacricetodon del Aragoniense y Vallesiense (Mioceno) de la Península Ibérica

MEMORIA PARA OPTAR AL GRADO DE DOCTOR

PRESENTADA POR

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Director

Pablo Peláez-Campomanes de Labra

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La ilustración de la portada es una creación de Óscar Sanisidro. El resto de ilustraciones utilizadas en esta memoria son creaciones de Iñaki Oliver, Itziar San Vicente, Enrique Cantero y Francisco Gascó. Cada autor permanece como propietario intelectual de cada una de sus ilustraciones.

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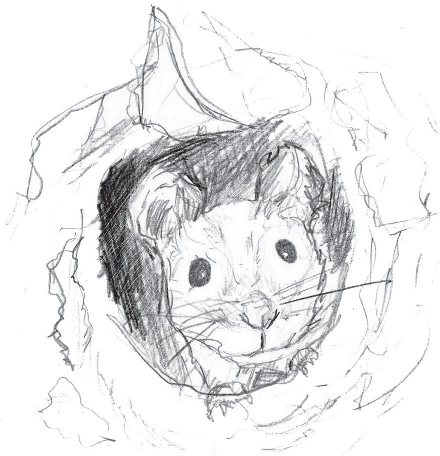

Memoria de Tesis Doctoral presentada por
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bajo la dirección del doctor
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A mi familia y amigos

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RESUMEN

Evolución del género *Megacricetodon* del Aragoniense y Vallesiense (Mioceno) de la Península Ibérica

Introducción

Esta Tesis doctoral presenta la evolución del cricétido *Megacricetodon* (Rodentia, Mammalia) desde su aparición en el Aragoniense inferior (Mioceno inferior) hasta su extinción en el Vallesiense inferior (Mioceno superior). Debido a su amplia distribución geográfica (toda Eurasia) y su gran diversidad de especies de rango estratigráfico relativamente reducido, *Megacricetodon* es uno de los principales taxones utilizados como indicadores bioestratigráficos del Mioceno continental europeo. De hecho, la aparición y evolución de sus diferentes especies ha sido utilizada para definir la mayoría de las biozonas locales y unidades biocronológicas del Aragoniense y Vallesiense inferior de Europa.

La principal cuenca de estudio de este trabajo es la Cuenca de Calatayud-Montalbán (Zaragoza, España), que destaca por su gran abundancia y riqueza del registro paleontológico. Además la excelente exposición de los yacimientos así como la superposición estratigráfica de los sedimentos fosilíferos ha permitido datar numéricamente la mayoría de los yacimientos paleontológicos, lo que convierte a esta cuenca en una de las más idóneas de la Península Ibérica.

Objetivos

El objetivo principal de esta Tesis doctoral es profundizar en el conocimiento del género *Megacricetodon* en la Península Ibérica, a través del estudio y la descripción del nuevo material disponible de la Cuenca de Calatayud-Montalbán.

Un aumento en el conocimiento sistemático de *Megacricetodon* resulta fundamental debido a su utilidad bioestratigráfica y biocronológica. Por lo tanto es fundamental estudiar y describir el material existente de este género, así como, evaluar cada una de las especies que están incluidas en los diferentes linajes de *Megacricetodon* de la Península Ibérica.

Resulta especialmente importante la revisión del linaje *Megacricetodon primitivus – M. ibericus*, ya que constituye uno de los principales indicadores bioestratigráficos del Mioceno para las faunas españolas. Además, un mayor conocimiento de las especies españolas de *Megacricetodon* nos permitirá realizar comparaciones con otras especies europeas del mismo género, a fin de proponer un contexto paleobiogeográfico y filogenético de este género en Europa.

Además hay que cumplir unos objetivos parciales a fin de poder comprender mejor la evolución de las especies del género *Megacricetodon* en la Península Ibérica y consecuentemente proponer un contexto paleobiogeográfico más preciso de este grupo en Europa.

El primero de ellos, consiste en describir el material de *Megacricetodon* de la zona local Db. Ésta especies es muy importante desde el punto de vista de la bioestratigrafía española.

El segundo consiste en tratar de solucionar el problema del linaje *M. primitivus – M. collongensis*. Para ello se estudiarán y revisarán las especies *Megacricetodon primitivus* y *M. collongensis*.

Finalmente, el último linaje que se estudiará es el de *M. crusafonti – M. ibericus*, de gran importancia en la Península Ibérica debido a su elevado y continuo registro estratigráfico, así como a su abundancia relativa (*Megacricetodon* constituye el 95% de la fauna de roedores).

Resultados

Para esta Tesis, se han estudiado, descrito y medido 13.771 elementos dentales de *Megacricetodon*, procedentes de 75 localidades de la Cuenca de Calatayud-Montalbán y de 38 localidades europeas, de un periodo de edad comprendido entre el Aragoniense inferior (Mioceno inferior) y el Vallesiense inferior (Mioceno superior).

Para ello se ha confeccionado una matriz morfológica con los principales caracteres de los elementos dentales, calculándose la frecuencia de los estados de carácter para las diferentes asociaciones de *Megacricetodon* de la Cuenca de Calatayud-Montalbán. Además se ha actualizado la nomenclatura de *Megacricetodon* para los diferentes elementos yugales.

Los resultados obtenidos de los análisis de los patrones métricos y morfológicos han sido interpretados taxonómicamente. Estos resultados se han comparado con otras poblaciones de *Megacricetodon* procedentes de diferentes cuencas europeas proponiéndose un nuevo contexto paleobiogeográfico. Además esta revisión de la evolución de *Megacricetodon* nos ha permitido refinar la bioestratigrafía del Aragoniense y del Vallesiense inferior.

Conclusiones taxonómicas

En esta Tesis se han descrito y estudiado 9 especies de *Megacricetodon* proponiéndose tres nuevas especies.

Megacricetodon vandermeuleni sp. nov. es una especie de gran talla presente en la zona local Db (Aragoniense Medio). El material estudiado procede de cinco localidades de la Cuenca de Calatayud-Montalbán (Zaragoza) y una localidad de la Cuenca de Loranca (Cuenca). Esta nueva especie presenta una gran importancia bioestratigráfica debido a que está restringida a la biozona Db. Además coexistió con el pequeño *Megacricetodon primitivus*.

Megacricetodon vandermeuleni presenta una morfología similar a otros taxones de *Megacricetodon* de Europa Central, lo que nos ha permitido proponer un nuevo grupo europeo, el "*Megacricetodon bavaricus* group" que incluye las especies *Megacricetodon* aff. *collongensis*, *M. bavaricus*, *M.* aff. *bavaricus*, *M. bezianensis*, *M. lappi*, *M. aunayi* y *M. vandermeuleni*. Este grupo habría aparecido en Francia, Suiza y Alemania durante la MN 4, dispersándose por el Suroeste de Europa en la MN 5.

Se ha asignado a la especie *Megacricetodon primitivus* el material de *Megacricetodon* de edades comprendidas entre el Aragoniense inferior y el Aragoniense medio, desde la biozona Ca hasta la biozona Db. El patrón evolutivo observado en esta especie permanece estable a lo largo del tiempo tanto en talla como en morfología dental, aunque con gran variación intra-poblacional.

La colección tipo de esta especie, Valtorres, ha sido nuevamente estudiada y descrita, y se propone una correlación de esta fauna con la biozona Da. Los análisis llevados a cabo en el material muestran grandes deformaciones tafonómicas que afectan seriamente a la variabilidad métrica de la población de *Megacricetodon*.

Las comparaciones con otras poblaciones europeas indican que la distribución geográfica de *Megacricetodon primitivus* está restringida al suroeste de Europa, y más concretamente a la Península Ibérica y Francia.

Megacricetodon alvarezae sp. nov. es una nueva especie de talla media que ha sido descrita en yacimientos del Aragoniense medio (parte superior de la biozona Db y biozona Dc) de la Cuenca de Calatayud-Montalbán. Esta nueva especie mantiene su morfología dental inalterada a lo largo del tiempo, aunque muestra una ligera disminución de tamaño en las localidades más antiguas.

Proponemos una hipótesis filogenética para esta especie relacionándolo con *Megacricetodon primitivus.* En Portugal, *Megacricetodon primitivus* habría evolucionado hacia una morfología similar a *Megacricetodon alvarezae* sp. nov., migrando hacia España al final de la biozona Db (MN 5). En la biozona local Dc, esta especie sería la forma de *Megacricetodon* más común. Esta nueva especie sería endémica de la Península Ibérica, restringida únicamente a España y Portugal.

Megacricetodon collongensis ha sido descrita en las localidades de la parte baja de la biozona Dd, mientras que la especie de talla grande, *Megacricetodon gersii*, ha sido reconocida en la parte alta de la biozona Dd y en la E. El estudio del material de *Megacricetodon* procedente de 37 localidades de la Cuenca de Calatayud-Montalbán nos ha permitido interpretar que estás dos especies pertenecen a dos formas sucesivas dentro del mismo linaje.

El material de *Megacricetodon collongensis* español, es más similar morfológicamente al material de *M. collongensis* de Vieux-Collonges, que al de *M. "collongensis"* de Port-la-Nouvelle, lo que soportaría la existencia del linaje *M. collongensis - M. gersii*. La evolución de una especie en otra está marcada por cambios en la morfología dental y un aumento en la talla. En la Cuenca de Calatayud-Montalbán, estos cambios ocurrieron al mismo tiempo que uno de los principales cambios sedimetológicos de la cuenca.

Con respecto a *Megacricetodon gersii*, en esta Tesis hemos asignado el material de las localidades del Aragoniense medio (biozona Dd y E) a esta especie, en lugar de al material de las localidades de la parte alta del Aragoniense (biozonas F y G1), como se pensaba anteriormente. Este cambio en la asignación específica tiene importantes implicaciones bioestratigráficas y biocronológicas, ya que *M. gersii* de la Península Ibérica precedería a *M. gersii* de Suiza, cambiando tanto la dirección de migración de esta especie (ahora de Europa del Oeste a Europa Central), como la magnitud de la diacronía (de 400 ky a 200ky).

Además, proponemos un nuevo grupo, el "*Megacricetodon primitivus* group" que incluiría las especies *M. primitivus, M. alvarezae, M. collongensis* y *M. gersii*.

Megacricetodon bilbilis sp. nov. es una nueva especie de talla grande presente en las biozonas E (Aragoniense medio), F y G1 (Aragoniense superior). Formaría parte del linaje *Megacricetodon bilbilis – M. crusafonti - M. crusafonti-ibericus – M. ibericus.* Este linaje aparecería en España con la especie *M. bilbilis* sp. nov. durante la parte superior de la zona loca E, dispersándose durante las biozonas F y G1, y evolucionando a *M. crusafonti* en la biozona G2. La última aparición de este linaje ocurriría en la zona local H (Vallesiense inferior) con la especie *M. ibericus*. La especie *Megacricetodon gersii* ha sido excluida de este linaje basado en las importante diferencias (tanto métricas como morfológicas) que hay entre ellos, así como, basado en la coexistencia de *M. gersii* y *M. bilbilis* sp. nov. en varias localidades de la Cuenca de Calatayud-Montalbán.

La distribución geográfica de este linaje estaría restringida a la Península Ibérica, aunque posiblemente habría alcanzado Francia.

Conclusiones paleogeográficas

La entrada del género *Megacricetodon* en Europa dejaría de ser un bioevento único, ya que al menos habría entrado a través de tres olas de migración:

La primera ola que se puede reconocer es la migración del *Megacricetodon* griego. Son formas de talla pequeña endémicas del área griega, cuyo registro aparece en la MN 4 inicial.

La segunda ola de migración consistiría en el grupo del *Megacricetodon bavaricus*. Estas formas de talla grande se distribuyen principalmente en cuencas Centro-Europeas. Este grupo no habría alcanzado la Península Ibérica hasta mitad de la MN 5.

La tercera ola sería la migración del grupo *Megacricetodon primitivus*. Este grupo habría aparecido en Francia en la MN 4 (Aragoniense inferior), dispersándose por España y Portugal al final de la MN 4, y alcanzando Suiza en la MN 5 (Aragoniense medio).

Finalmente, se puede reconocer el linaje *Megacricetodon bilbilis – M. ibericus*. Estas formas de talla grande serían endémicas del Suroeste de Europa, registrándose por primera vez en España en el Aragoniense medio.

ABSTRACT

Evolution of *Megacricetodon* from the Aragonian and Vallesian (Miocene) from the Iberian Peninsula

Introduction

This dissertation presents the evolution of the cricetid *Megacricetodon* (Rodentia, Mammalia) since its first occurrence in the lower Aragonian (early Miocene) till its last occurrence in the lower Aragonian (upper Miocene). *Megacricetodon* is one of the main taxa used as biostratigraphic markers of the continental Miocene in Europe, owing to its wide geographical distribution (Eurasia) and the high diversity of species with relatively short stratigraphic range. In fact, the first appearance and evolution of its different species have been used to define the majority of the local zones and biochronological unities for the Aragonian and lower Vallesian of Europe.

The Calatayud-Montalbán Basin (Zaragoza, Spain) is the main basin of this study. This basin stands out for its abundance and richness of paleontological record. Besides, the excellent outcrops of the sites and the stratigraphic superposition of the fossiliferous sediments, allow to asses a numerically dating to most of the paleontological sites, what makes the Calatayud-Montalbán Basin one of the most suitable basins of the Iberian Peninsula.

Objetives

The main objective of this dissertation is to deepen in the knowledge of the genus *Megacricetodon* in the Iberian Peninsula, through the study and description of the new available material from the Calatayud-Montalbán.

A systematic knowledge of *Megacricetodon* is important because of its bioestratigraphical and biochronological utility. Therefore, it is fundamental to study and

describe the *Megacricetodon* material, as well as, to evaluate each of the species that are included in the different lineages of the Iberian Peninsula.

The revision of the lineage *Megacricetodon primitivus – M. ibericus* is especially important, owing to it constitutes one of the main bioestratigraphic markers of the Miocene for the Spanish faunas. In addition, a better understanding of the Spanish species, will allow us to realize comparisons with other European *Megacricetodon* species, in order to propose a paleobiogeographic and philogenetic framework of this genus in Europe.

Besides, it is necessary to fulfill partial objectives in order to have a better understanding of the *Megacricetodon* species of the Iberian Peninsula, and consistently propose a more precise phylogeographical framework of this group in Europe.

The first of them, consist in describing the material of *Megacricetodon* from the local zone Db. This new species is very important from the Spanish bioestratigraphy.

The second is to seek to resolve the problem of *Megacricetodon primitivus-M. collongensis lineage*. For this purpose, the species *Megacricetodon primitivus* and *M. collongensis* are studied and revised.

Finally, the last lineage studied, is the lineage *M. crusafonti – M. ibericus*, which is very important in the Iberian Peninsula owing to its high and continuous estratigraphic record, and its high relative abundance (*Megacricetodon* may constitute up to 95% of the rodent faunas).

Results

In this dissertation, 13.771 dental elements of *Megacricetodon* from 75 localities of the Calatayud-Montalbán Basin and from 38 European localities, have been studied, described and measured, from lower Aragonian (early Miocene) to lower Vallesian (upper Miocene).

A morphological matrix has been made with the main characters of the dental elements, calculating the frequency of the character states in the different *Megacricetodon* assemblages from the Calatayud-Montalbán Basin. Besides, the nomenclature of the cheek teeth of *Megacricetodon* has been updated.

The results obtained from the analyses of the metrical and morphological patterns, have been interpreted taxonomically. These results have been compared with other *Megacricetodon* assemblages from other European basins, allowing us to propose a new paleobiogeographic framework. Besides, the revision of the *Megacricetodon* evolution has let us refine the bioestratigraphy of the Aragonian and early Vallesian.

Taxonomical conclusions

In this Thesis, 9 *Megacricetodon* species have been studied and described, proposing three new ones.

Megacricetodon vandermeuleni sp. nov. is a large-sized species from the local zone Db (middle Aragonian). The studied material is from five localities of the Calatayud-Montalbán Basin (Zaragoza) and one locality of the Loranca Basin (Cuenca). This new species is biostratigraphicaly important because it is restricted to biozone Db. Besides, it coexisted with the small *Megacricetodon primitivus*.

Megacricetodon vandermeuleni is morphologically close to other *Megacricetodon* taxa from central Europe, which have led us to propose a new European group of *Megacricetodon* the "*Megacricetodon bavaricus* group" which includes: *Megacricetodon* aff. *collongensis*, *M. bavaricus*, *M.* aff. *bavaricus*, *M. bezianensis*, *M. lappi*, *M. aunayi* and *M. vandermeuleni*. This group occurs in France, Switzerland and Germany during MN 4, dispersing through Southwestern Europe during MN 5.

It has been assigned to the small-sized *M. primitivus* the material of *Megacricetodon* from early to middle Aragonian, from biozone Ca to biozone Db. The observed evolutionary patterns of this specie are stable through time in size and dental morphology, although with high intra-populational variability.

The type collection of this species, Valtorres, have been restudied and described, proposing the correlation of this fauna to the local zone Da. The analyses carried out on the material shows strong taphonomical deformations that seriously affect the metrical variability of this *Megacricetodon* assemblage.

The comparisons with other European assemblages indicate that the geographical distribution of *Megacricetodon primitivus* is restricted to Southwestern Europe, and specifically the Iberian Peninsula and France.

Megacricetodon alvarezae sp. nov. is a new medium-sized species, described in localities from middle Aragonian (uppermost part of biozone Db and biozoneDc) of the Calatayud-Montalbán Basin. This new species maintains its dental morphology unchanged through time although exhibits a slightly decrease in size from oldest localities.

The phylogenetic hypothesis proposed for this species, related it with *Megacricetodon primitivus*. In Portugal, *Megacricetodon primitivus* evolved towards a morphology similar to *Megacricetodon alvarezae* sp. nov., migrating into Spain at the end of the biozone Db (MN 5). In the local zone Dc this species is the most common *Megacricetodon*. This new species is an endemic Iberian species, restricted to Portugal and Spain.

Megacricetodon collongensis have been described in the localities from the lower part of the biozone Dd, whereas the large-sized *Megacricetodon gersii* have been recognized in the upper part of local zone Dd and E. The study of the *Megacricetodon* material of 37 localities from the Calatayud-Montalbán Basin allows us to propose that these species are two successive forms within a single lineage.

The Spanish material of *Megacricetodon collongensis* is morphologically similar to the material from *M. collongensis* from Vieux-Collonges, instead to *M. "collongensis"* from Port-la-Nouvelle, which support the existence of the lineage *M. collongensis - M. gersii*. The evolution from one species to the other is marked by changes in the dental morphology and by an increase in size. In the Calatayud-Montalbán Basin, these changes occurred at the same time of one of the main sedimentological changes in the Basin.

Regarding to *Megacricetodon gersii,* in this dissertation we have assigned to this species the material from the middle Aragonian localities (biozones Dd and E), instead of that from the upper Aragonian (local zone F and G1) as previously thought. This change in the specific assignation have important bioestratigraphical and biochronological implications, owing to *M. gersii* from the Iberian Peninsula predates its occurrence to Switzerland, changing the direction of the migration of this species (now from Western Europe to Central Europe) and also changing the magnitude of the diachrony (from 400ky to 200 ky).

In addition, we propose the "*Megacricetodon primitivus* group", which includes *M. primitivus, M. alvarezae*, *M. collongensis* and *M. gersii*.

Megacricetodon bilbilis sp. nov. is anew large-sized species from biozones E (middle Aragonian), F and G1 (upper Aragonian). This species is part of the lineage *Megacricetodon bilbilis – M. crusafonti - M. crusafonti-ibericus – M. ibericus.*

This lineage occurs in Spain with the species *M. bilbilis* sp. nov. during the upper part of local zone E, spreading during biozones F and G1, and evolving into *M. crusafonti* in local zone G2. The species *Megacricetodon gersii* has been excluded of this lineage, based on important differences (morphological and metrical) found between them, as well as, based on the co-occurrence of *M. gersii* and *M. bilbilis* sp. nov. in several localities in the Calatayud-Montalbán Basin.

The geographical distribution of this lineage is restricted to the Iberian Peninsula and it may appear in France.

Paleogeographical conclusions

The entrance of *Megacricetodon* in Europe would no longer be a single bioevent, since at least it would have entered in three migration waves:

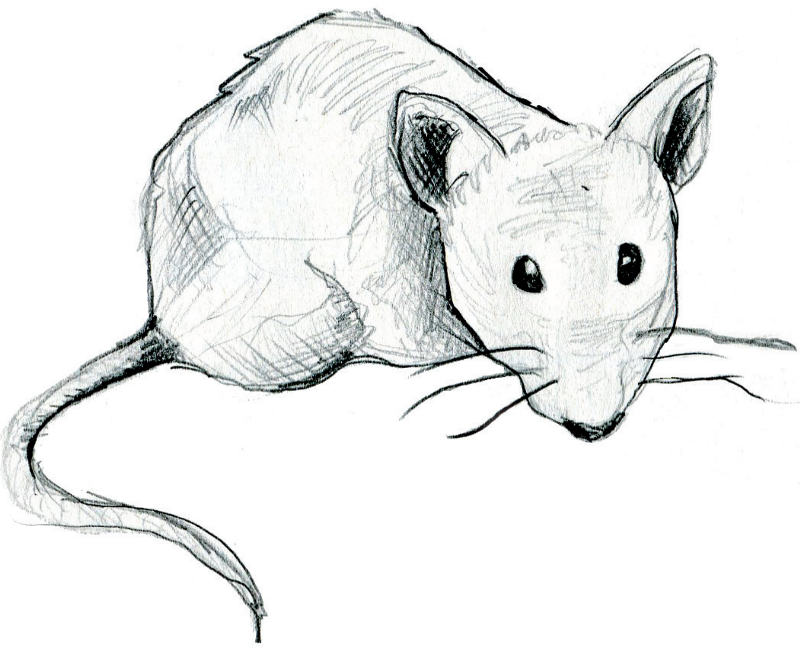
The first wave that it is possible to recognize is the migration of the Greek *Megacricetodon*. These small-sized forms were endemic of the Greek area and are recorded from the earliest MN 4.

The second migration wave is the *Megacricetodon bavaricus* group. These large-sized forms of *Megacricetodon* were mainly distributed in the Central-European basins. This group will not reach the Iberian Peninsula till middle MN 5.

The third wave is the migration of the *Megacricetodon primitivus* group. This group occur in France in MN 4 (lower Aragonian) dispersing into Spain and Portugal at the end of the MN 4, and reaching Switzerland in the MN 5 (middle Aragonian).

Finally, it is possible to recognize the lineage *Megacricetodon bilbilis – M. ibericus*. These large-sized forms are endemic of the Southwestern Europe, first recorded in Spain in middle Aragonian.

1. Introduction



1. 1. INTRODUCTION

Megacricetodon Fahlbusch, 1964 (Cricetidae, Rodentia) is an important rodent genus, since it is highly diverse and abundant, during most of the European Miocene. This cricetid of small size lived during the Aragonian and early Vallesian, all over Eurasia. Its extinction at the early Vallesian coincided with the entry of the first murids in Western Europe.

Owing to the wide geographical distribution and the high diversity of species with relatively short stratigraphic range, *Megacricetodon* is one the most characteristic biostratigraphic markers of the continental Miocene faunas in Europe. The first appearance and evolution of different species of *Megacricetodon* in combination with other taxa have been used to define the majority of the local biozones and biochronological unities for the Aragonian and lower Vallesian of Europe (Mein 1975; de Bruijn et al., 1992; Aguilar 1995; Daams et al., 1999; van der Meulen et al., 2012).

Megacricetodon is a very common element of the Spanish small mammals. It fossil association may constitute up to 95% of the rodent faunas (Daams & Freudenthal, 1988). In the Spanish Miocene, 11 species of *Megacricetodon* have been cited, eight of which have been defined in various Spanish basins (Calatayud-Montalbán Basin, Duero Basin, Vallès-Penedès).

The Calatayud-Montalbán Basin stands out for its abundance and richness of paleontological record. Since the 60s, numerous geological and paleontological studies in the continental sediments of this basin have been carried out. The excellent outcrops and stratigraphic superposition of the fossiliferous sediments allowed the discovery of numerous paleontological sites in the Calatayud-Montalbán Basin, being approximately 120 localities known up to date (Daams et al., 1999, Van Dam et al., 2006).

The main goal of this work is deepening in the knowledge of the genus *Megacricetodon* through the study and description of the new material available of representatives from the Calatayud Montalbán Basin. The knowledge of the Spanish *Megacricetodon* will allow comparison with representatives of this genus from other European geographical areas and therefore, facilitate the proposal of paleobiographical and phylogenetic frameworks for this genus in Europe.

1.2. BACKGROUND OF THE GENUS Megacricetodon

In 1964, Fahlbusch, proposed and defined the name *Megacricetodon* as a subgenus within the new genus *Democricetodon*. This author proposed *Megacricetodon gregarius* (Shaub, 1925) as type species and included a number of species previously assigned to the genus *Cricetodon*: *M. minor* (Lartet 1851), *M. bourgeoisi* (Schaub 1925), *M. ibericus* (Schaub 1944), *M. collongensis* (Mein, 1958) and *M. lappi* (Mein, 1958).

In the early 70s, Mein and Freudenthal (1971) considered different genus both *Megacricetodon* and *Democricetodon* granted them this category. These authors presented a list of species assigned to *Megacricetodon* including *M. primitivus* (Freudenthal, 1963), *M. crusafonti* (Freudenthal, 1963), and the species assigned to this genus by Fahlbush in 1964 *M. gregarius*, *M. minor*, *M. bourgeoisi*, *M. ibericus*, *M. collongensis*, *M. bavaricus*, *M. similis*, *M. minutus*, *M. debruijni* and *Megacricetodon* sp. from Vieux-Collonges.

Since them, many new forms of *Megacricetodon* have been described, increasing the number of species included in this genus until the current 40:

M. aguilari Lindsay, 1988

M. andrewsi Peláez-Campomanes & Daams, 2002

M. aunayi Lazzari & Aguilar, 2007

M. bavaricus (Fahlbusch, 1964)

M. beijiangensis Maridet et al., 2011

M. bezianensis Bulot, 1980

M. bourgeoisi (Schaub, 1925)

M. collongensis (Mein, 1958)

M. crisiensis Radulescu & Samson, 1988

M. crusafonti (Freudenthal, 1963)

M. daamsi Lindsay, 1988

M. drebruijni Freudenthal, 1968

M. dzhungaricus Kordikova & De Bruijn, 2001

M. fahlbuschi Aguilar et al., 1999

M. freudenthali García Moreno (in Álvarez-Sierra & García-Moreno, 1986)

M. fournasi Aguilar, 1995

M. germanicus Aguilar, 1980

M. gersii **Aguilar, 1980**

M. gregarius (Schaub, 1925) **Type species**

M. ibericus (Schaub, 1944)

M. lalai Aguilar et al., 1999

M. lappi (Mein, 1958)

M. lemartinelli Aguilar, 1995

M. lopezae García Moreno (in Álvarez-Sierra & García-Moreno, 1986)

M. minor (Lartet, 1851)

M. minutus Daxner, 1967

M. mythikos Lindsay, 1988

M. primitivus (Freudenthal, 1963)

M. pussillus Qiu, 1996

M. rafaeli Daams & Freudenthal, 1988

M. robustus Kälin & Engesser, 2001

M. roussillonensis Aguilar et al., 1986w

M. similis (Fahlbusch, 1964)

M. sinensis Qiu et al., 1981

M. sivalensis Lindsay, 1988

M. tautavelensis Lazzari & Aguilar, 2007

M. vandermeuleni Oliver & Peláez-Campomanes, 2013

M. wuae Aguilar et al., 1999

M. yei Bi et al., 2008

M. yenicekentensis Erten et al., 2014

Of all the species of *Megacricetodon* known to date, 29 out of 40 are European species. Of which, eleven of these species have been cited in localities of the Spanish Miocene (in bold). Furthermore, almost 30% of the European species have been defined based on material of the Spanish localities. The Calatayud-Montalbán Basin is the most prominent Spanish basin, the excellent exposure and the stratigraphic superimposition of the fossiliferous sediments have allowed define five type localities of *Megacricetodon* (Armantes 7, Fuente Sierra 4, Manchones 1, Pedregueras 2C and Valtorres), the Duero

Basin has two (Simancas 2 and Ampudias), and finally the Vallès-Penedès Basin has one type locality (Hostalets de Pierola) (See Table 1.1.1).

***Megacricetodon* species**	**Type locality**	**Spanish Basin**
M. debruijni	Pedregueras 2C	Calatayud-Montalbán
M. crusafonti	Manchones 1	Calatayud-Montalbán
M. rafaeli	Armantes 7	Calatayud-Montalbán
M. primitivus	Valtorres	Calatayud-Montalbán
M. vandermeuleni	Fuente Sierra 4	Calatayud-Montalbán
M. freudenthali	Ampudia 9	Duero
M. lopezae	Simancas 2	Duero
M. ibericus	Hostalets de Pierola	Vallès-Penedès

Table 1.1.1. *Megacricetodon* species defined in Spanish basins.

Many authors have proposed different phylogenetic hypothesis for the genus *Megacricetodon*, depending on the knowledge they have of it: Fahlbusch, 1964, Sesé Benito, 1977; Aguilar, 1980; 1995; Aguilar et al., 1986; 1999; Alvarez-Sierra & García-Moreno, 1986; Garcia-Moreno, 1987; Daams & Freudenthal, 1988; Lazzari & Aguilar, 2007.

Regarding the material from the Calatayud-Montalbán Basin, stand out the works of Freudenthal (1963; 1968), who was the first to recognize the biostratigraphic use of the succesive evolutionary stages of the *Megacricetodon primitivus - M. ibericus* lineage. Daams & Freudenthal (1988) made a review of all the available material of *Megacricetodon* from this basin, defining a new species (*Megacricetodon rafaeli*), and evaluating the evolution of this genus in a biogeographical, stratigraphical and paleoecological context. These authors also suggested that *Megacricetodon primitivus* (Freudenthal, 1963) is part of the lineage that evolved into *M. collongensis* (see Figure 1.1.1). However, subsequent works in the Calatayud-Montalbán Basin (Daams et al., 1998; 1999), suggested the synonymy of *M. primitivus* with *M. collongensis*, and *M. collongensis–crusafonti* with *M. gersii*, although this is not formally proposed (see Figure 1.1.1). In the last decade, the increment of fossil sites in the Calatayud-Montalbán Basin, has allowed greatly increase the study of the Miocene rodent fauna. Thus, the different works on *Megacricetodon* (Oliver Perez et al., 2008; Oliver et al., 2009 a, b) proposed that the two species are different. In 2012, Van der Meulen et al., published an update in the biostratigraphy of the lower and middle Aragonian, formally redefining the Spanish local zones, and determining the distribution of the small mammals for the Miocene European Chronology.

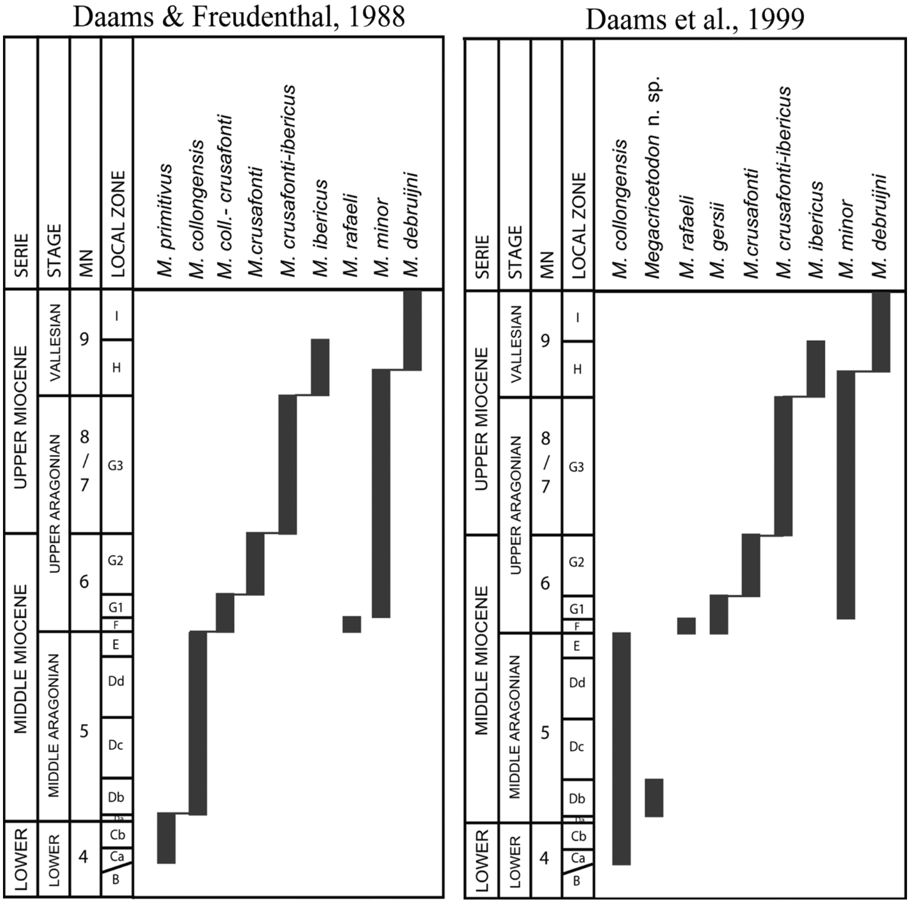


Figure 1.1.1. Distribution ranges of the *Megacricetodon* species from the Calatayud-Montalbán Basin. On the left, after Daams & Freudenthal, 1988; on the right, after Daams et al., 1999.

In this work, we have only focused on the large-sized lineage of *Megacricetodon*, the "Iberian" species. The small-sized species (*M. rafaeli* and the *M. minor-M. debruijni* lineage), which come from Central Europe, are a very controversial and complicated group of *Megacricetodon*, which would need their own revision. Unfortunately, both the large amount of available material and the remoteness of the material (France, Germany, Switzerland, Czech Republic…) make this work unmanageable within this thesis, and therefore have been left out.

1.3. GEOLOGICAL CONTEXT OF THE CALATAYUD-MONTALBÁN BASIN

The Neogene Calatayud-Montalbán Basin is located in the Iberian Range (NE of the Iberian Peninsula) (see Figure 1.2.1). It is a narrow depression, with NW-SE direction and approximately 125 Km long and 12 Km wide. It is bounded by Paleozoic and Mesozoic reliefs (Daams et al., 1999) and is filled by Tertiary terrestrial deposits, ranging in age from Early Miocene to Early Pliocene, which thickness has not been precisely determined. The basin borders contain coarse alluvial fan clastics, such as conglomerates, sandstones, silts and clays. While the central zones of the basin contain lacustrine sediments, such as evaporites and carbonates (Marín, 1932).

This basin shows a complex tectonic structure, with variations depending on the area (Julivert, 1954; Ferreiro & Ruiz, 1991; Anadón & Moissenet, 1996). In the vicinity of Catalayud, north of the basin, the structure is a system of grabens, associated to normal faults. Whereas, the SW margin of the basin is bounded by directional tectonics, the Jiloca Fault, which is a strike-slip faults, trending NW-SE direction, and is associated to low-angle trusting of Cambrian materials of the Hercinic basement, which slices over the alluvial deposits of early to middle Miocene age (Colomer & Santanach, 1988).

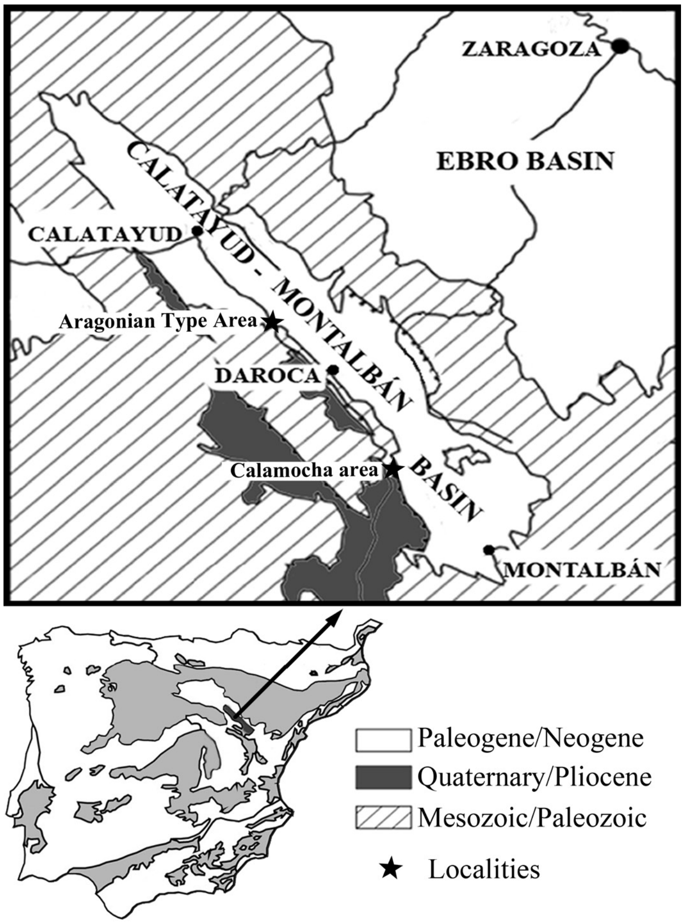


Figure 1.2.1. Map of the Tertiary continental basin of the Iberian Peninsula. In dark gray the studied area of the Calatayud-Montalbán Basin is represented. Modified from Álvarez Sierra et al., (2003).

The Calatayud-Montalbán Basin is one of the tertiary Spanish basins with major richness and abundance of Miocene mammal fossils of the world, especially micromammals (with more than 100 fossil sites), as well as, for the quality of the sedimentary record (four main sections correlated lithologically, magnetostratigraphy and biostratigraphically) (Daams et al., 1999, Van der Meulen et al., 2012). This has served for the definition of two stratotypes of continental Tertiary section, the Ramblian (part of the lower Miocene)

Figure 1.2.2. Detailed geological map of the Aragonian type area. Main units and fossil localities are indicated (Daams et al., 1999).

near Calamocha (province of Teruel) and the Aragonian (part of the Lower Miocene and Middle Miocene) near Villafeliche (province of Zaragoza) (Daams et al., 1977; 1987).

The Aragonian type area is situated along the Rambla de Vargas near the locality of Villafeliche(Figure 1.2.2). Over a Paleozoic basement (Cambrian age), composed of slates, quartzites and calcareous schists, the Neogene materials are disconformablely located. There are three principal units (Figure 1.2.3): Valdemoros-Vargas Unit, Las Umbrias Unit and Las Planas Unit (Daams et al., 1999).

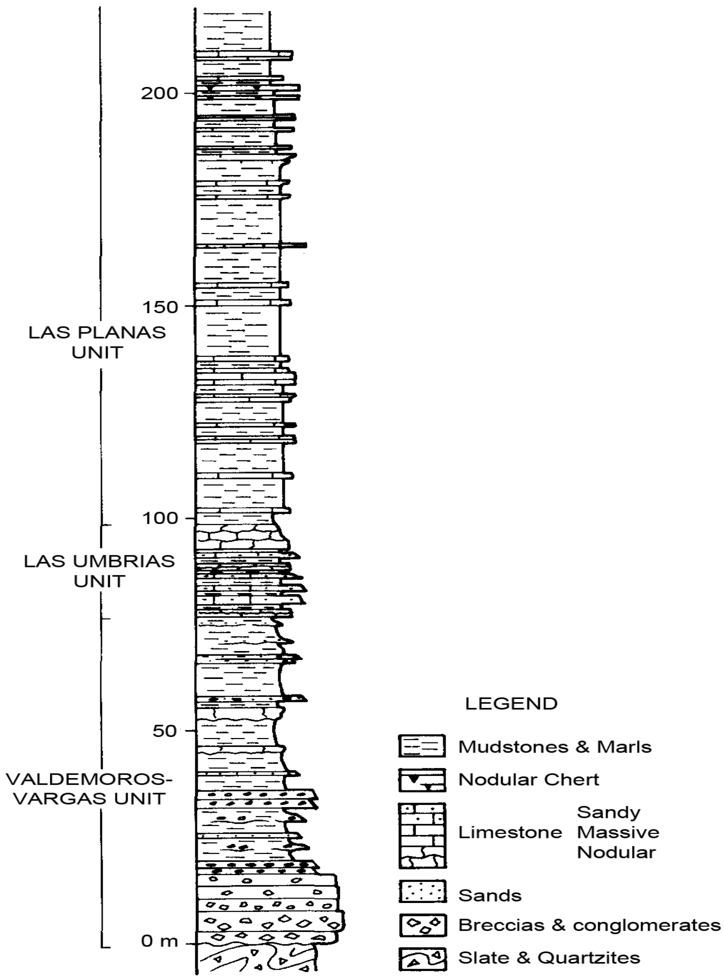


Figure 1.2.3. Synthetic litological log of the main units defined within the Aragonian type area (Daams et al., 1999).

The Valdemoros-Vargas Unit (Figure 1.2.4), contains in its lower part, an interbedded of red mudstones, gravels and sandstones. The upper part is formed by levels of nodular limestones and greyish marls, which gradually remain to the upper unit (Alcalá et al., 2000). It is interpreted as an alluvial fan complex less developed that evolved to distal parts of alluvial fans with shallow carbonated lakes. The mudstones interbedded with nodular carbonates represent a deposition in very shallow lakes with frequent subaerial exposure, as shown by desiccation cracks (Sanz et al., 1995). The vertebrate remains are found isolated in gravel to coarse-grained sandfill channels in the lower part of this unit (Daams et al., 1999).

Las Umbrias Unit (Figure 1.2.5) is formed by tufaceous limestones, nodular carbonates (sandy micrites, desiccation cracks and bioturbation traces) and green to grey marlstones, where most of the fossiliferous localities of the section are found (Daams et al., 1999). It was interpreted (Alonso Zarza et al., 1992; Platt & Wright, 1992) as small and shallow lakes and marshes which underwent episodic subaerial exposure (paludal environment).

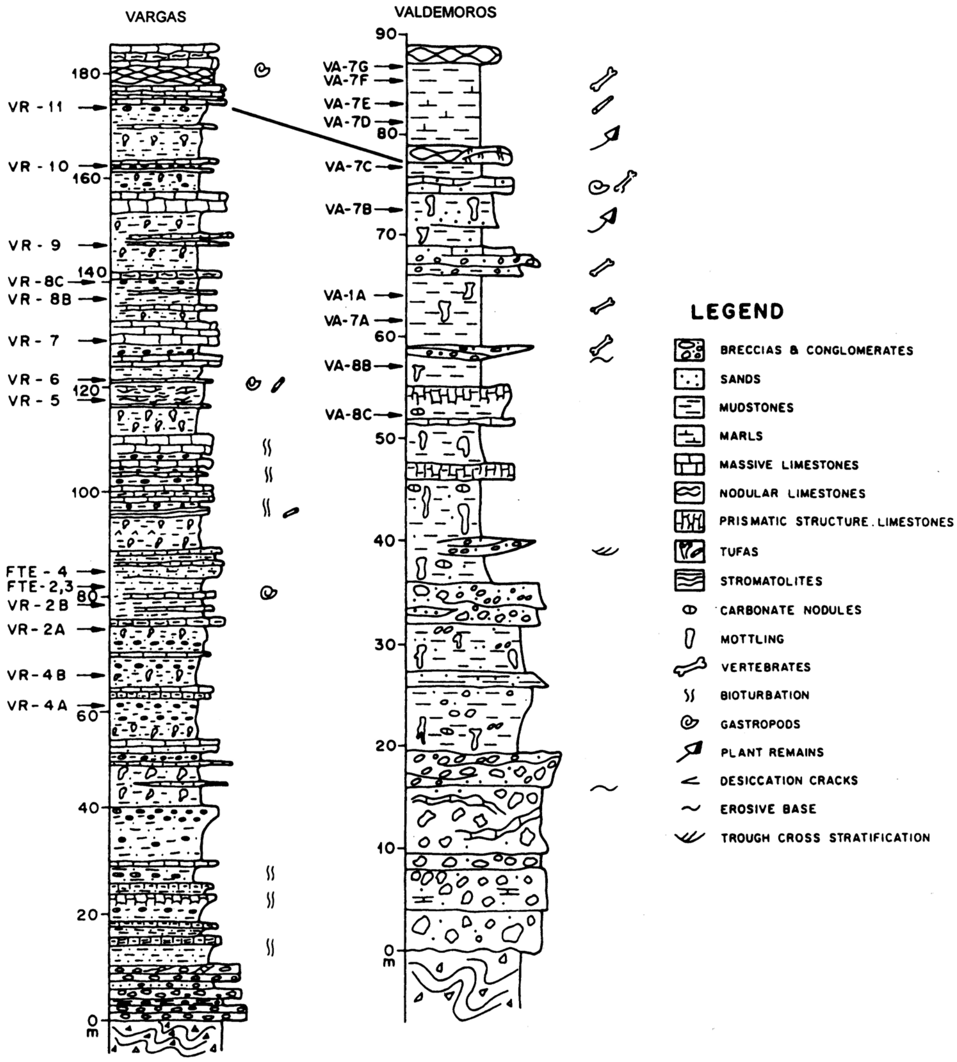


Figure 1.2.4. Litological log of the Valdemoros-Vargas Unit (Daams et al., 1999).

Las Planas Unit (Figure 1.2.5) comprises a succession of red mudstones with interbedded marls and limestones. Sanz et al., (1995) suggested that the marls and carbonates were deposited in very shallow lakes of ponds which underwent frequent exposure. Many fossiliferous localities are found in the reddish mudstone beds of the section (Daams et al., 1999).

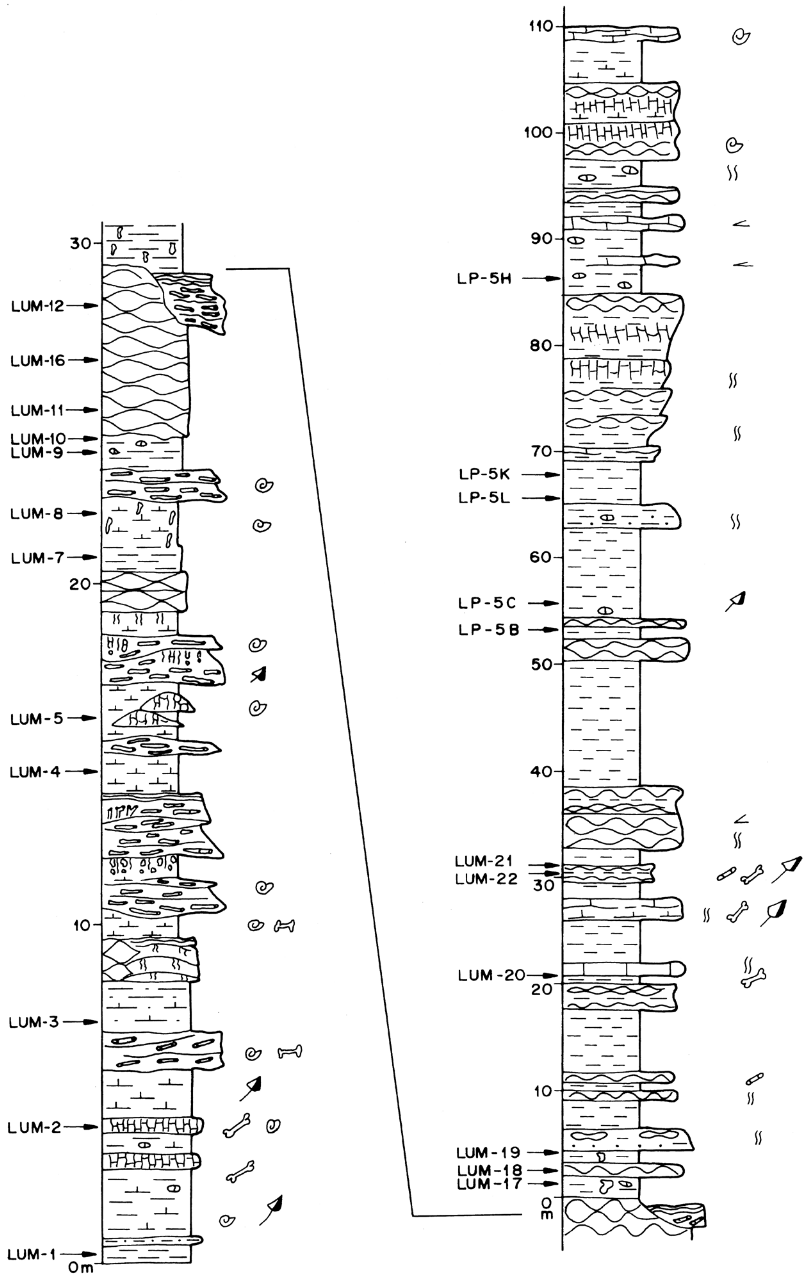


Figure 1.2.5. Litological log of the Las Umbrias-Las Planas Unit (Daams et al., 1999).

1.4. OBJECTIVES

One of the main objectives of this Thesis is to understand the evolution of the genus *Megacricetodon* in the Iberian Peninsula. A systematic knowledge of this genus is important considering that the first appearance and evolution of different species of *Megacricetodon* in combination with other taxa have been used to define the majority of the local biozones and biochronological units for the Miocene.

Therefore, it is fundamental to study and describe the existing material of this genus as well as evaluate each of the species which are included in the different lineages of *Megacricetodon* from the Iberian Peninsula. It is especially important the revision of the *M. primitivus-M. ibericus* lineage. This lineage has special interest given that is one of the most characteristic biostratigraphic markers of the Miocene Spanish faunas. Furthermore, the Spanish *Megacricetodon* species have been compared with the European ones, in order to propose a paleobiogeographic framework.

In addition to the main objective there are partial ones that have to be fulfilled in order to understand the evolution of the genus in Spain. In this way, the first partial objective will be to describe the material of *Megacricetodon* from the local zone Db. This large-sized *Megacricetodon* is of importance for Spanish biostratigraphy. Furthermore, we proposed the "*M. bavaricus* group". The European species included in this group are: *M.* aff. *collongensis*, *M. bavaricus*, *M.* aff. *bavaricus*, *M. bezianensis*, *M. lappi*, *M. aunayi* and *M. vandermeuleni*. The proposed *Megacricetodon* group is very useful for European faunal correlations and timing of migration events.

The second partial objective deals with the problem of *Megacricetodon primitivus - M. collongensis lineage*. The objective is to clarify the status of *Megacricetodon primitivus* and determine the geographical distribution of this species. As mentioned above, Daams & Freudenthal (1988) suggested that *Megacricetodon primitivus* (Freudenthal, 1963) evolved into *M. collongensis*. However, Daams et al., (1998; 1999), informally proposed that *M. primitivus* and *M. collongensis* were synonymous. Posterior works (Oliver Perez et al., 2008; Oliver et al., 2009 a, b; Van der Meulen et al., 2012) rejected the synonymy between this two species. For that purpose, we have restudied and described the type material of *M. primitivus* from the locality of Valtorres and other localities from the Calatayud-Montalbán Basin not previously described. Furthermore, we have compared it with other assemblages of *M. primitivus* from European basins, showing the evolutionary patterns of this species.

Megacricetodon collongensis is a conflictive species difficult to recognize with certitude in the Spanish Miocene. Therefore, in this work we will try to explain and understand the status of *Megacricetodon collongensis*, studying and describing the *Megacricetodon* forms during the early and middle Miocene from the Calatayud-Montalbán Basin. Furthermore, the Spanish material have been compared to the type locality of Vieux-Collonges and with other assemblages assigned to *M. collongensis*.

As mentioned before, the large-sized lineage *Megacricetodon collongensis - M. crusafonti* (after Daams & Freudenthal, 1988) is one of the main *Megacricetodon* lineages of the Iberian Peninsula, due to its high and continuous stratigraphical record (middle to upper Miocene), as well as for the high abundance and number of fossils recorded (95% of the rodent fauna).

All those partial objectives will also help to understand the evolution of the *Megacricetodon* species from the Calatayud-Montalbán Basin within the evolution of the genus and consequently to propose a more precise paleobiogeographical framework of this group in Europe based on the obtained results.

1.5. DISTRIBUTION OF THE CHAPTERS OF THIS THESIS

The Thesis consists of different chapters that focus on the evolution of the genus *Megacricetodon* from the Calatayud-Montalbán Basin, since its first occurrence in the lower Aragonian till its disappearance in the lower Vallesian.

The chapters have been structured in order to solve the different partial objectives previously presented.

In this way, chapter 3 is dedicated to the description of the species *Megacricetodon vandermeuleni* from the local zone Db, which has been defined by Oliver & Peláez-Campomanes in 2013 (published in the Journal of Vertebrate Paleontology), an integrated into the *M. bavaricus* group.

The chapters from 4 to 7 are dedicated to the *Megacricetodon* forms that were included in the *M. primitivus - M ibericus* lineage (*M. primitivus - M. collongensis - M. crusafonti - M. ibericus*) defined by Daams & Freudenthal (1988).

Chapter 4 focuses on the species *Megacricetodon primitivus* (explaining this complex species, redefining the type material, including the new material discovered, and clearing up the time span of this species (published by Oliver & Peláez-Campomanes in Palaeontographica Abteilung A).

Chapter 5 focuses on a new large-sized *Megacricetodon* species that occurred at the end of local zone Db co-occurring with *M. primitivus* and *M. vandermeuleni* and get extinct at the end of local zone Dc.

Chapter 6 is dedicated to the species from MN5. The small-sized *Megacricetodon collongensis* occurred during the lower part of the local zone Dd in the Calatayud-Montalbán Basin, disappearing in the middle of this zone. The larger-sized *Megacricetodon gersii* is restricted to the upper part of the MN5, being its first occurrence during the upper part of the local zone Dd and disappearing at the end of the local zone E.

Chapter 7 focused in the *Megacricetodon* material of the *M. crusafonti - M. ibericus* lineage from the upper Aragonian and lower Vallesian and discuss their relationships with the older forms described in the Calatayud-Montalbán basin.

Finally, chapter 8 is a synthesis of the main results and ideas obtained with this thesis. Pointing out the evolutionary patterns of the different species of *Megacricetodon* in the Calatayud-Montalbán Basin, and their relationships with other European *Megacricetodon* species contributing to propose a more detailed European paleobiogeografic framework.

1.6. REFERENCES

Aguilar, J. 1980. Nouvelle interpretation de l'evolution du genre *Megacricetodon* au cours du Miocene. Paleovertebrata Volumen Jubilaire R. Lavocat:355-366.

Aguilar, J., G. Clauzon, and J. Michaux. 1999. Nouveaux Cricétidés (Rodentia, Mammalia) dans le Miocène moyen de la région de Digne (Alpes de Haute Provence) Systématique, Biocronologie, Corrélations. Paleontographica 253:1-28.

Aguilar, J. P. 1995. Evolution de la lignée *Megacricetodon collongensis-Megacricetodon rousillonensis* (Cricetidae, Rodentia, Mammalia) au cours du Miocène inférieur et moyen dans le sud de la France. Palaeovertebrata 24:1-45.

Aguilar, J. P., M. Calvet, and J. Michaux. 1986. Découvertes de faunes de micromammifères dans les Pyrénées Orientales (France) de l'Oligocène supérieur au Miocène supérieur; espèces nouvelles et réflexion sur l'étalonnage des échelles continentale et marine. Comptes Rendus de l'Académie des Sciences de Paris Sér. II 303:755-760.

Alcalá, L., A. Alonso-Zarza, M. Álvarez-Sierra, B. Azanza, J. Calvo, J. Cañaveras, J. v. Dam, M. Garcés, W. Krijgsman, A. v. d. Meulen, P. Pélaez-Campomanes, Pérez-González.A, S. Sánchez Moral, R. Sancho, and E. Sanz Rubio. 2000. El registro sedimentario y faunístico de las cuencas de calatayud-daroca y teruel. evolución paleoambiental y paleoclimática durante el neógeno. Revista de la Sociedad Geológica de España 13:323-343.

Alonso-Zarza, A. M., J. P. Calvo, and M. A. Carcía del Cura. 1992. Palustrine sedimentation and associated features-granification and pseudo-microkarst- in the Middle Miocene (Intermediate Unit) of the Madrid Basin, Spain. Sedimentary Geology 76:43-62.

Alvarez-Sierra, M. A., and E. García-Moreno. 1986. New Gliridae and Cricetidae from the Middle and Upper Miocene of the Duero Basin, Spain. Studia Geologica Salmanticensia 22:145-189.

Alvarez-Sierra, M. A., J. P. Calvo, J. Morales, J. Alonso Zarza, B. Azanza, I. García Paredes, M. Hernández Fernández, A. v. d. Meulen, P. Pélaez-Campomanes, V. Quiralte, M. J. Salesa, I. M. Sánchez, and D. Soria. 2003. El tránsito Aragoniense-Vallesiense en el área de Daroca-Nombrevilla (Zaragoza, España). Coloquios de Paleontología, Vol. Ext. 1:25-33.

Anadón, P., and E. Moissenet. 1996. Neogene basins in the Eastern Iberian Range; pp. 68-76 *i*n P. F. Friend, and C. J. Dabrio (eds.), Tertiary basins of Spain, the stratigraphic record of crustal kinematics. Cambridge University Press.

Bi, S., J. Meng, and W. Wu. 2008. A new species of Megacricetodon (Cricetidae, Rodentia, Mammalia) from the Middle Miocene of northern Junggar Basin, China. American Museum Novitates 3602:1-23.

Bruijn, H. d., R. Daams, G. Daxner-Höck, V. Fahlbusch, L. Ginsburg, P. Mein, and J. Morales. 1992. Report of the RCMNS working group on fossil mammals, Reisensburg 1990. Newsletters of Stratigraphy 26:65-118.

Bulot, C. 1980. Nouvelle description de deux especes du genre *Megacricetodon* (Cricetidae, Rodentia) du Miocene de Bezian (Zone de La Romieu). Bulletin du Museum National d'Histoire Naturelle Section C Sciences de la Terre Paleontologie Geologie Mineralogie 2:3-16.

Colomer, M., and P. Santanach. 1988. Estructura y evolución del borde sur-occidental de la Fosa de Calatayud-Daroca. Geogaceta 4:29-31.

Daams, R., L. Alcalá, M. A. Alvarez Sierra, B. Azanza, J. A. van Dam, A. J. van der Meulen, J. Morales, M. Nieto, P. Peláez-Campomanes, and D. Soria. 1998. A stratigraphical framework for Miocene (MN4-MN13) continental sediments of central Spain. Comptes Rendus de l'Academie des Sciences, Serie II. Sciences de la Terre et des Planetes 327:625-631.

Daams, R., and M. Freudenthal. 1988. Cricetidae (Rodentia) from the type-Aragonian; the genus *Megacricetodon*; pp. 39-132 *in* M. Freudenthal (ed.), Biostratigraphy and paleoecology of the Neogene micromammalian faunas from the Calatayud-Teruel Basin (Spain). Scripta Geologica, Special Issue 1, Leiden.

Daams, R., M. Freudenthal, and M. Alvarez-Sierra. 1987. Ramblian: a new stage for continental deposits of early Miocene age. Geologie en Minjbouw 65:297-308.

Daams, R., M. Freudenthal, and A. Weerd, van de. 1977. Aragonian, a new stage for continental deposits of Miocene age. Newsletters of Stratigraphy 6:42-55.

Daams, R., A. J. van der Meulen, M. A. Álvarez-Sierra, P. Peláez-Campomanes, J. P. Calvo, M. A. Alonso Zarza, and W. Krijgsman. 1999. Stratigraphy and sedimentology of the Aragonian (Early to Middle Miocene) in its type area (North-Central Spain). Newsletters on Stratigraphy 37:103-139.

Daxner, G. 1967. Ein neuer cricetodontide (Rodentia, Mammalia) aus dem Pannon des Wiener Beckens. Annalen des Naturhistorischen Museums in Wien 71:27-36.

Erten, H., S. Sen, and M. Gormus. 2014. Middle and Late Miocene Cricetidae (Rodentia, Mammalia) from Denizli Basin (Southwestern Turkey) and a new species of Megacricetodon. Journal of Paleontology, 88(3):504-518.

Fahlbusch, V. 1964. Die Cricetiden (Mam.) der Oberen Süsswasser-Molasse Bayerns. Bayerische Akademie Wissenschaften. Mathematisch-naturwissenschaftliche Klasse. Munchen 118:1-135.

Ferreiro, E., and V. Ruiz. 1991. Memoria y Mapa geológico 1/200.000, Daroca (Hoja 40). Instituto Geológico y Minero, Madrid.

Freudenthal, M. 1963. Entwicklungsstufen der Miozänen Cricetodontinae (Mam. Rod.). In *Mittelspaniens und ihre Stratigraphische Bedeutung*, pp. 107. Ricks University, Utrecht.

Freudenthal, M. 1968. On the mammalian fauna of the Hipparion beds in the Calatayud-Teruel basin Part IV: The genus Megacricetodon (Rod.). Proceedings of the Koninklijke Nederlandse Akademie Van Wetenschappen, sér. B 71:57-72.

García-Moreno, E. 1987. El genero *Megacricetodon* (Cricetidae, Rod.) en el Aragoniense y Vallesiense de la Cuenca del Duero. Relaciones filogeneticas. Col-Pa 41:51-106 ?

Julivert, M. 1954. Observaciones sobre la tectónica de la Depresión de Calatayud. Arrahona:3-18.

Kälin, D., and B. Engesser. 2001. Die Jungmiozäne Säugetierfauna vom Nebelbergweg bei Nunningen (Kanton Solothurn, Schweiz). Schweizerische Paläontologische Abhandlungen 121:1-61.

Kordikova, E. G., and H. de Bruijn. 2001. Early Miocene rodents from the Aktau Mountains (south-eastern Kazakhstan). Senckenbergiana Lethaea 81:391-405.

Lartet, E. 1851. Notice sur la colline de Sansan. Portes, Auch:1-47.

Lazzari, V., and J. P. Aguilar. 2007. Les *Megacricetodon* du gisement karstique miocène moyen de Blanquatère 1 (Pyrénées-Orientales, Sud de la France): nouvelles espèces, implications biochronologique et phylogénetique. Geobios 40:91-111.

Lindsay, E. H. 1988. Cricetid rodents from Siwalik deposits near Chinji Village: part 1: Megacricetodontinae, Myocridetontinae and Dendromurinae. Paleovertebrata 18:95-154.

Maridet, O., W.-Y. Wu, J. Ye, S.-D. Bi, X.-J. Ni, and J. Meng. 2011. Early Miocene cricetids (Rodentia) from the Junggar basin (Xinjiang, China) and their biochronological implications. Geobios (Villeurbanne) 44.

Marín, A. A. 1932. Sondeos de investigación de sales potásicas. Boletín de Sondeos 3.

Mein, P. 1958. Les mammifères de la faune sidérolithique du Vieux -Collonges. Nouvelles Archives du Muséum d'Histoire Naturelle de Lyon 5:1-122.

Mein, P. 1975: Biozonation du Néogène Mediterranéen à partir des Mammifères. Paper presented at the VIth Congress of the R.C.M.N.S., Bratislava , Slowakia, 1975.

Mein, P., and M. Freudenthal. 1971. Une nouvelle classification des Cricetidae (Mam. Rod.) du Tertiaire d'Europe. Scripta Geologica 2:1-37.

Morales, J., L. Alcalá, M. Hoyos, P. Montoya, M. Nieto, B. Pérez, and D. Soria. 1993. El yacimiento del Aragoniense medio de La Retama (Depresión Intermedia, provincia de Cuenca, España): significado de las faunas con Hispanotherium. Scripta Geologica 103:23-39.

Morales, J., M. Nieto, P. Peláez-Campomanes, D. Soria, M. A. Álvarez Sierra, L. Alcalá, L. Amezua, B. Azanza, E. Cerdeño, R. Daams, S. Fraile, J. Guillem, M. Hoyos, L. Merino, I. de Miguel, R. Monparler, P. Montoya, B. Pérez, M. J. Salesa, and I. M. Sánchez. 1999. Vertebrados continentales del Terciario de la cuenca de Loranca (Provincia de Cuenca); pp. 237-260 *in* E. Aguirre, and I. Rábano (eds.), La huella del pasado: Fósiles de Castilla-La Mancha. Junta de Comunidades de Castilla-La Mancha, Toledo.

Oliver, A., I. García-Paredes, and P. Pelaez-Campomanes. 2009a. A geometric morphometric analysis of *Megacricetodon* (Cricetodontinae, Rodentia, Mammalia) from the Db Biozone, Middle Aragonian. Paleontologia i Evolucio Memòria especial 3:101-102.

Oliver, A., P. López-Guerrero, I. García-Paredes, M. A. Álvarez Sierra, and P. Pelaez-Campomanes. 2009b. Evolution of *Megacricetodon* tooth pattern through geometric morphometrics analysis. Journal of Vertebrate Paleontology 29:158A.

Oliver, A., and P. Pelaez-Campomanes. 2013. *Megacricetodon vandermeuleni*, sp. nov. (Rodentia, Mammalia), from the Spanish Miocene: a new evolutionary framework for Megacricetodon. Journal of Vertebrate Paleontology 33:943-955.

Oliver Pérez, A., P. López-guerrero, and P. Pelaez-Campomanes. 2008. Primer representante del género *Megacricetodon* de la Cuenca de Calatayud-Daroca (Zaragoza, España); pp. 317-329 *in* J. Esteve, and G. Meléndez (eds.), Palaeontológica Nova. Publicaciones del Seminario de Paleontología de Zaragoza, Zaragoza.

Peláez-Campomanes, P., and R. Daams. 2002. Middle Miocene rodents from Pasalar, Anatolia, Turkey. Acta Palaeontologica Polonica 47:125-132.

Platt, N. H., and V. P. Wright. 1992. Palustrine carbonates and the Florida Everglades: Towards an exposure index for the fresh-water environment? Journal of Sedimentary Research 62:1058-1071.

Qiu, Z. 1996. Middle Miocene micromammals faunas from Tunggur, Nei, Mongolia. 216 pp. Beijing Science Press.

Qiu, Z., C. Li, and S. Wang. 1981. Miocene mammalian fossils from Xining Basin, Qinghai. Vertebrata Palasiatica 19:156-173.

Radulescu, C., and P. Samson. 1988. Les cricetides (Rodentia, Mammalia) du Miocene (Astaracien superieur) de Roumanie. Travaux de l'Institut de Speologie "Emile Racovitza" 27:67-78.

Sanz, M. E., A. M. Alonso Zarza, and J. P. Calvo. 1995. Carbonate pond depsoits related to semi-arid alluvial systems: examples from the tertiary Madrid Basin, Spain. Sedimentology 42:437-452.

Schaub, S. 1925. Die Hamsterartige Nagetiere des Tertiärs und ihre lebenden Verwandten. Abhandlungen des Schweizerischen paläontologische Gesellschaft = Mémoires de la Société paléontologique suisse 45 (Années1921-25):1-114.

Schaub, S. 1944. Cricetodontiden der Spanischen Halbinsel. Eclogae Geologicae Helvetiae. Lausanne 37:453-457.

Sese Benito, C. 1977. Los Cricetidos (Rodentia, Mammalia) de las fisuras del Mioceno medio de Escobosa de Calatañazor (Soria, España). Trabajos sobre Neógeno-Cuaternario 8:127-180.

van Dam, J. A., H. Abdul Aziz, M. A. Álvarez-Sierra, F. J. Hilgen, L. W. van den Hoek Ostende, L. J. Lourens, P. Mein, A. J. van der Meulen, and P. Peláez-Campomanes. 2006. Long-period astronomical forcing of mammal turnover. Nature, 443(7112):687-691.

van der Meulen, A. J., I. García-Paredes, M. A. Álvarez-Sierra, L. W. van den Hoek Ostende, K. Hordijk, A. Oliver, and P. Peláez-Campomanes. 2012. Updated Aragonian biostratigraphy: Small Mammal distribution and its implications for the Miocene European Chronology. Geologica Acta 10:159-179.

2. Material and Methods

2. 1. MATERIAL AND METHODS

2.1.1. MATERIAL

In the present work, 13.771 dental specimens of *Megacricetodon* have been studied and described.

Most of the available material of *Megacricetodon* has been recovered from the Calatayud-Montalbán Basin. The studied assemblages have been collected in numerous field campaigns by an interdisciplinary Dutch and Spanish team (Daams et al., 1999).

The table 2.1.1 shown the 98 localities studied, the number of teeth analyzed, the abbreviations of each fossil sites, the numerical age of the different localities proposed by Daams et al., 1999, Van Dam et al., 2006 and Van der Meulen et al., 2012; the local zone proposed for the sites, the Neogene Mammal units (MN) described by Mein (1975), the stage and the series for each fossil site.

The specimens described are stored at the Museo Nacional de Ciencias Naturales-CSIC (Madrid, Spain), the Nationaal Natuurhistorisch Museum-Naturalis (Leiden, The Netherlands) and the Faculty of Earth Sciences, Utrecht University (Utrecht, The Netherlands).

Furthermore, other European *Megacricetodon* material had been studied and described in order to compare with the Spanish. This material are from numerous European localities (as shown in table 2.1.2) stored in France: Université Claude Bernard Lyon 1, Université Montpelier 1 and Muséum National d'Histoire Naturelle of Paris; Germany: Bayerische Staatssammlung für Palaontologie und Geologie München (Munich); and Switzerland: Naturhistorisches Museum Basel.

2.1.2. METHODS

The systematic study is based on the analysis of the occlusal surface of fossil dental elements, since the teeth are usually well preserved, because they are the most mineralized part of the skeleton. Furthermore, most of the taxonomy of the fossil rodents are based on the teeth, because their morphological features are very distinctive and diagnostic.

The nomenclature of the cheek teeth of *Megacricetodon* (see Figure 2.2.1 and Figure 2.2.2) is based on Oliver & Peláez-Campomanes (2013). Notation M/m is used for upper/lower molars respectively.

SERIES	STAGE	MN	ZONE	AGE Ma	SITE	ABBR.	N. TEETH
UPPER	VALLESIAN	9	I	10,010	Pedregueras 2A	PED2A	78
			H	10,770	Nombrevilla 1	NOM1	
				11,33	Carrilanga 1	CAR1	
MIDDLE MIOCENE	UPPER ARAGONIAN	7/8	G3	12,01	Solera	SOL	
				12,56	Toril 1	TOR1	
				12,6	Las Planas 5H	LP5H	
				12,7	Alcocer 2	AC2	
				12,85	Villafeliche 9	VL9	
		6	G2	13,08	Las Plans 5K	LP5K	31
				13,160	Las Planas 5L	LP5L	
					Arrollo del Val 6	AV6	31
				13,2	Borjas	BOR	
				13,250	Manchones	MAN	
			G1	13,300	Valalto 1B	VT1B	62
				13,350	Valalto 1A	VT1A	
				13,550	Las Planas 5C	LP5C	157
				13,560	Las Planas 5B	LP5B	327
			F	13,680	Valalto 2C	VL2C	
				13,700	Valalto 2B	VL2B	
				13,740	Armantes 7	ARM7	
				13,750	Las Umbrias 21	LUM21	
				13,760	Las Umbrias 22	LUM22	193
	MIDDLE ARAGONIAN	5	E	13,800	Las Umbrias 20	LUM 20	128
				13,950	Las Umbrias 19	LUM19	143
				13,960	Las Planas 4BA	LP4BA	156
				13,990	Las Umbrias 14	LUM14	107
				14,000	Las Umbrias 18	LUM18	41
				14,010	Las Umbrias 17	LUM17	55
				14,030	Las Umbrias 12	LUM12	166
				14,040	Las Umbrias 16	LUM16	146
				14,060	Las Umbrias 11	LUM11	319
			Dd	14,090	Las Umbrias 10	LUM10	62
				14,180	Las Umbrias 9	LUM9	73
				14,190	Regajo 2	RG	
				14,200	Las Umbrias 8	LUM8	128
				14,205	Las Umbrias 7	LUM7	82
				14,240	Valdemoros 7G	VA7G	15
				14,270	Valdemoros 7F	VA7F	79
				14,290	Valdemoros 7E	VA7E	99
				14,300	Las Umbrias 5	LUM5	33
				14,320	Las Umbrias 4	LUM4	91
				14,330	Valdemoros 7D	VA7D	31
				14,370	Las Umbrias 3	LUM3	70
				14,380	Vargas 11	VR11	32
				14,400	Las Umbrias 2	LUM2	50
MIDDLE MIOCENE	MIDDLE ARAGONIAN	5	Dd	14,420	Las Umbrias 1	LUM1	46
				14,500	Valdemoros 3F	VA3F	103
				14,530	Valdemoros 3E	VA3E	205
				14,550	Valdemoros 7C	VA7C	118
				14,590	Valdemoros 7B	VA7B	112
				14,610	Valdemoros 1A	VA1A	124
				14,620	Valdemoros 7A	VA7A	77
				14,670	Valdemoros 8B	VA8B	20
				14,690	Valdemoros 8C	VA8C	29
				14,710	Vargas 8C	VR8C	173
				14,730	Vargas 8B	VR8B	214
				14,750	Casetón 2B	CS2B	25
				14,780	Casetón 1A	CS1A	202
				14,810	Vargas 7	VR7	364
				14,820	Valdemoros 3D	VA3D	179
			Dc	15,490	Villafeliche 4B	VL4B	90
				15,500	Villafeliche 4A	VL4A	308
				14,840	Valdemoros 3B	VA3B	280
				15,200	Valdemoros 11	VA11	36
				15,250	Vargas 6	VR6	200
				15,320	Vargas 5	VR5	173
				15,350	Valdemoros 9	VA9	5
					Munebrega 3A	MUN3A	137
			Db	15,680	Valdemoros 8A	VA8A	208
				15,730	Moratilla 3	MOR3	33
				15,780	Moratilla 2	MOR2	126
				15,820	Fuente Sierra 4	FTE4	94
					La Retama	REM	447
				15,840	La Col D	COLD	318
			Da	15,860	La Col C	COLC	299
				15,880	La Col B	COLB	23
					Valtorres	VLT	199
				15,880	Fuente Sierra 3	FTE3	53
				15,890	Fuente Sierra 2	FTE2	48
				15,910	Olmo Redondo 9	OR9	57
				15,920	Vargas 2B	VR2B	50
				15,930	La Col A	COLA	45
LOWER MIOCENE	LOWER ARAGONIAN	4	Cb	15,940	Vargas 2A	VR2A	76
				15,950	Olmo Redondo 8	OR8	153
				15,980	Olmo Redondo 5	OR5	70
				16,100	Vargas 3	VR3	95
				16,110	Vargas 1A	VR1A	317
				16,120	Vargas 4BB	VR4BB	142
				16,130	Vargas 4B	VR4B	26
				16,150	Vargas 4A	VR4A	170
			Ca	16,300	Olmo Redondo 4A	OR4A	56
				16,330	San Roque 3	SR3	16
				16,490	Artesilla	ART	574

Table 2.1.1. Localities with fossil material studied in this work. The table shows the number of teeth analyzed, the abbreviations of each locality, the numerical age proposed by Daams et al., 1999, Van Dam et al., 2006 and Van der Meulen et al., 2012, the local zone proposed for the fossil sites, the Neogene Mammal units (MN), the stage and the series for each locality.

Megacricetodon	SITE	Country	Stored	F/C
M. primitivus	Chelas 1	Portugal	UCB Lyon 1	C
M. bezianensis	Pellecahus	France	UCB Lyon 1	C
M. primitivus	Pellecahus	France	UCB Lyon 1	C
M. bezianensis	Bézian	France	UCB Lyon 1	C
M. primitivus	Bézian	France	UCB Lyon 1	C
M. bezianensis	La Romieu-Soucaret	France	UCB Lyon 1	C
M. primitivus	La Romieu-Soucaret	France	UCB Lyon 1	C
M. primitivus	La Romieu-Labadic	France	UCB Lyon 1	C
M. collongensis	Vieux-Collonges	France	UCB Lyon 1	F
M. lalai	Châteauredon	France	Université Montpellier 1	F
M. aunayi	Blanquatère 1	France	Université Montpellier 1	F
M. tautavelensis	Blanquatère 1	France	Université Montpellier 1	F
M. "collongensis-gersii"	Blanquatère 1	France	Université Montpellier 1	F
M. fournasi	Lo Fournas 2	France	Université Montpellier 1	F
M. rousillonensis	Lo Fournas 3	France	Université Montpellier 1	F
M. gersii	Lo Fournas 8	France	Université Montpellier 1	F
M. wae	Colombier bas	France	Université Montpellier 1	F
M. fahlbuschi	Estruguettes 6	France	Université Montpellier 1	F
M. germanicus	Collet Redom	France	Université Montpellier 1	F
M. gersii	Sansan	France	MNHN Paris, NMB Basel	F
M. minor	Sansan	France	MNHN Paris, NMB Basel	F
M. gregarius	La Grive-St-Alban	France	NMB Basel	F
M. robustus	Nebelbergweg	Switzerland	NMB Basel	F
M. similis	Anwil	Switzerland	NMB Basel	F
M. minor	Anwil	Switzerland	NMB Basel	F
M. germanicus	Anwil	Switzerland	NMB Basel	F
M. germanicus	Linn/Iberg	Switzerland	NMB Basel	F
Megacricetodon sp.	Eiboden	Switzerland	NMB Basel	F
M. aff. *collongensis*	Hirschthal	Switzerland	NMB Basel	F
M. aff. *collongensis*	Hubertingen	Switzerland	NMB Basel	F
M. aff. *collongensis*	Hüenerbach	Switzerland	NMB Basel	F
M. aff. *collongensis*	Tägernaustrasse	Switzerland	NMB Basel	F
M. aff. *collongensis*	Rauscheröd 1b	Germany	BSPGM Munich	F
M. aff. *collongensis*	Rauscheröd 1c	Germany	BSPGM Munich	F
M. aff. *collongensis*	Rembach	Germany	BSPGM Munich	F
M. aff. *collongensis*	Forsthart	Germany	BSPGM Munich	F
M. aff. *collongensis*	Günzburg U.	Germany	BSPGM Munich	F
M. bavaricus	Langenmoosen	Germany	BSPGM Munich	F
M. bavaricus	Bellenberg 1	Germany	BSPGM Munich	F
M. bavaricus	Bellenberg 2	Germany	BSPGM Munich	F
M. bavaricus	Attenfeld	Germany	BSPGM Munich	F
M. bavaricus	Niederaichbach	Germany	BSPGM Munich	F
M. bavaricus	Pöttmes	Germany	BSPGM Munich	F
M. germanicus	Adelschlag	Germany	BSPGM Munich	F
M. aff. *bavaricus*	Sandelzhausen	Germany	BSPGM Munich	F
M. minor	Sandelzhausen	Germany	BSPGM Munich	F
M. minor	Giggenhausen	Germany	BSPGM Munich	F
M. similis	Giggenhausen	Germany	BSPGM Munich	F

Table 2.1.2. European *Megacricetodon* samples compared to the Spanish material. The table shows the *Megacricetodon* species described, fossil site and country to which the studied species came from, the place where they are stored and if the studied collection is composed by fossils or casts. Abbreviations: **UCB Lyon 1**, Université Claude Bernard Lyon 1; **MNHN Paris**, National d'Histoire Naturelle of Paris; **NMB Basel**, Naturhistorisches Museum Basel; **BSPGM Munich**, Bayerische Staatssammlung für Palaontologie und Geologie München; **F**, Original fossil; **C**, Cast.

For the morphologic analysis 30 dental characters taken from the six molars (M1, M2, M3, m1, m2, m3) have been described, and selected based on their high variability. The different character states have been defined after Daams & Freudenthal (1988), Oliver & Peláez-Campomanes (2013), Oliver & Peláez-Campomanes (in press Palaeontogr Abt A, in press APP). The main character states used in this work are as follow:

Upper Molars

Anterocone of the M1 (Modified from Daams & Freudenthal, 1988 and Oliver & Peláez-Campomanes, 2013)

Data from specimens with moderate to high wear are not considered.

A. Slightly subdivided anterocone and the furrow is shallow.
B. Slightly subdivided anterocone, the furrow is shallow with a small platform in front of it.
C. Anterocone deeply split and the furrow reaches the crown basis.
D. Anterocone deeply split with a small platform in front of the furrow.
E. Anterocone deeply split with a small cingulum ridge in front it.

Division of the Anterocone of the M1 (from Oliver & Peláez-Campomanes, in press APP)

Data from specimens with moderate to high wear are not considered.

A. Anterocone with shallow subdivision.
B. Anterocone deeply subdivided. The furrow reaches the crown basis.

Anterior cingulum of the M1 (from Oliver & Peláez-Campomanes, in press APP)

Data from specimens with moderate to high wear are not considered.

A.There is not a platform or a cingulum in front of the anterocone.
B. There is a small platform in front of the anterocone.
C. There is a platform and a small cingulum ridge in front of the anterocone.

Symmetry of the Anterocone of the M1 (from Oliver & Peláez-Campomanes, 2013)

A. The labial and lingual cusps have similar size.
B. The labial cusp is larger than the lingual.
C. The labial cusp is smaller than the lingual.

Anterolophule of the M1 (from Oliver & Peláez-Campomanes, 2013)

A. The anterolophule connects to the middle of the two cones forming the anterocone.
B. The anterolophule connects to the lingual cusp.
C. The anterolophule connects to the labial cusp.

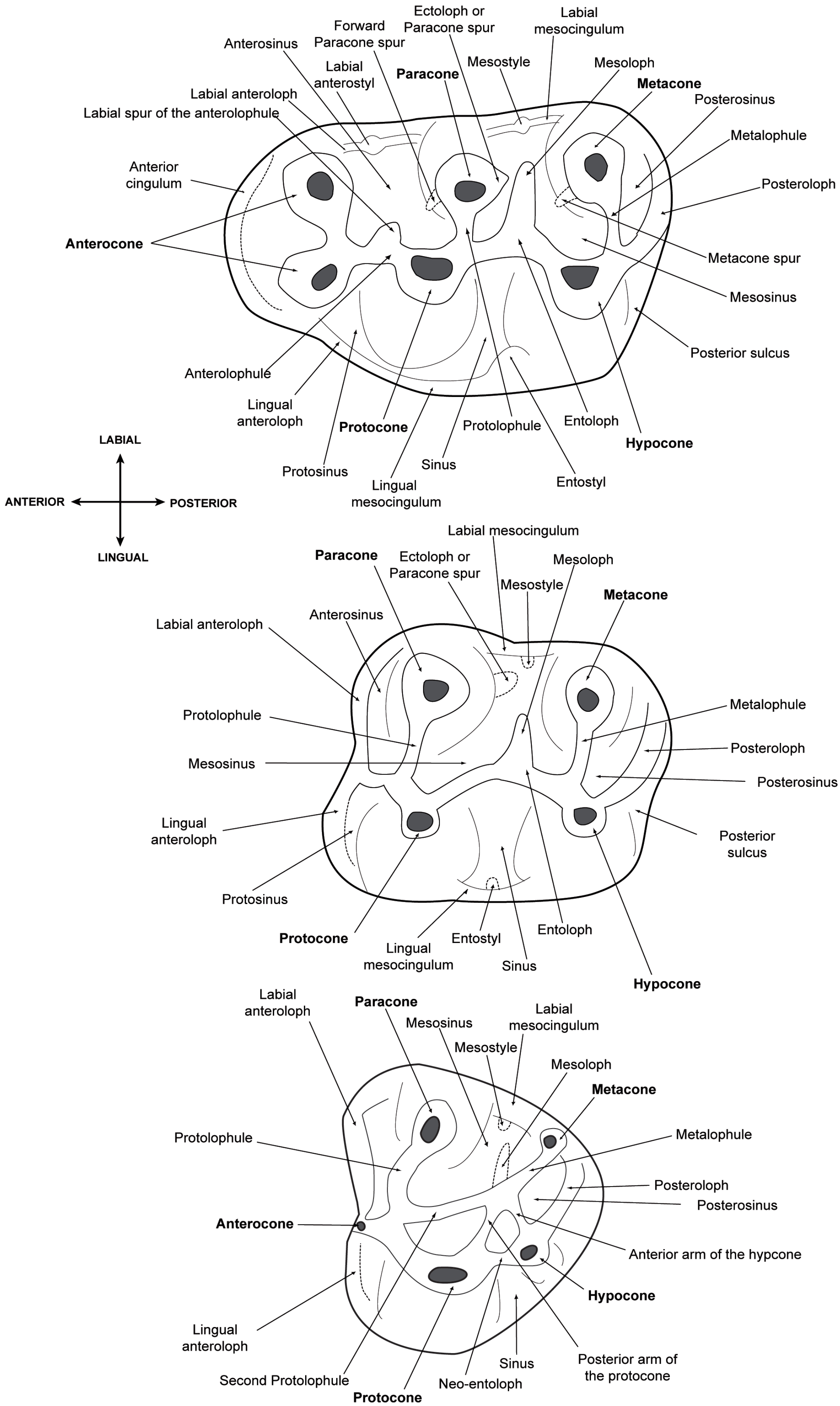


Figure 2.2.1. Nomenclature of the upper cheek teeth of *Megacricetodon*. Modified after Oliver & Peláez-Campomanes, 2013.

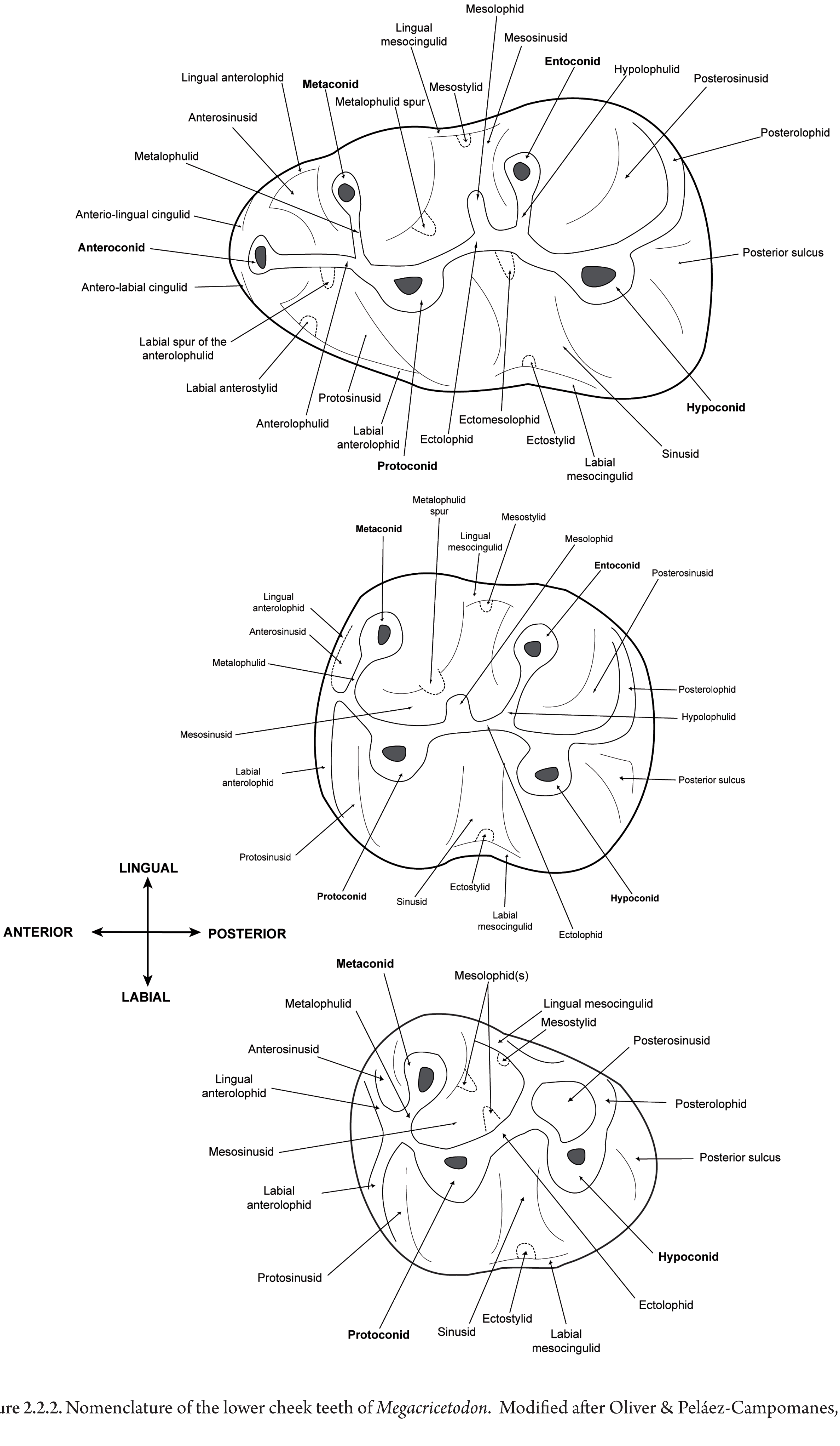


Figure 2.2.2. Nomenclature of the lower cheek teeth of *Megacricetodon*. Modified after Oliver & Peláez-Campomanes, 2013.

Labial Spur of the Anterolophule of the M1 (from Oliver & Peláez-Campomanes, 2013)

A. Present: There is a (short, medium or long) labial spur.

B. Incipient: There is an incipient labial spur.

C. Absent: The labial spur of the anterolophule is absent.

Protolophule of the M1 (Modified from Oliver & Peláez-Campomanes, 2013)

Not considered on specimens with strong wear.

A. Anterior: The protolophule is connected to the anterolophule in front of the protocone.

B. Transverse: The protolophule is transverse and connected to the protocone.

C. Transverse almost double: The protolophule is transverse and there is an incomplete posterior protolophule.

D. Posterior: The protolophule is posterior to the protocone.

E. Almost double: The protolophule is posterior almost double, form by the labial spur of the anterolophule or by the forward paracone spur.

F. Double: The protolophule is double.

Protolophule of the M2 (Modified from Daams & Freudenthal, 1988 and Oliver & Peláez-Campomanes, 2013)

Not considered on specimens with strong wear.

A. Anterior: The protolophule points forward and it is connected to the anterolophule in front of the protocone.

B. Anterior almost double: The anterior protolophule points forward and there is an incomplete posterior protolophule.

C. Transverse: The protolophule is transverse and connected to the protocone.

D. Transverse almost double: The protolophule is transverse and there is an incomplete posterior protolophule.

E. The protolophule is transverse but it is connected to the entoloph behind the protocone.

F. The entoloph is connected to the protocone indirectly through paracone and protolophule.

G. The entoloph is connected to the protocone indirectly through paracone and protolophule and also there is an incomplete posterior protolophule.

H. Double: There is a double protolophule.

I. Posterior: The protolophule points backwards and connects behind the protocone.

Protolophule of the M2 bis (Modified from Daams & Freudenthal, 1988 and Oliver & Peláez-Campomanes, 2013)

Not considered on specimens with strong wear.

A. Anterior: The protolophule points forward and it is connected to the anterolophule in front of the protocone.

B. Anterior almost double: The anterior protolophule points forward and there is an incomplete posterior protolophule.

C. Transverse: The protolophule is transverse and connected to the protocone.

D. Transverse almost double: The protolophule is transverse and there is an incomplete posterior protolophule.

E. The protolophule is transverse but it is connected to the entoloph behind the protocone.

F. The entoloph is connected to the protocone indirectly through paracone and protolophule.

G. The entoloph is connected to the protocone indirectly through paracone and protolophule and also there is an incomplete posterior protolophule.

H. Double: There is a double protolophule.

I. The protolophule is transverse and connected to the entoloph behind the protocone and also there is posterior protolophule.

J. The entoloph is connected to the protocone indirectly through paracone and protolophule and also there is posterior protolophule.

K. Posterior almost double: The protolophule points backwards and connects behind the protocone and also there is an incomplete anterior protolophule.

L. Posterior: The protolophule points backwards and connects behind the protocone.

Anterior Protolophule of the M2 (from Oliver & Peláez-Campomanes, 2013)

A. The protolophule is directed forwards or anterior almost double.

B. The transverse protolophule bents forwards before the connection with the protocone.

C. The forward-directed protolophule become transverse before the connection with the protocone.

Lingual mesocingulum of the M1 and M2 (from Oliver & Peláez-Campomanes, in press Palaeontogr Abt A)

A. The lingual mesocingulum could be present or not, but never connects the hypocone and the anterocone.

B. There is a strong lingual mesocingulum that connects the hypocone and the anterocone and runs lingual to the protocone.

Ectoloph (Paracone Spur) of the M1 and M2 (from Daams & Freudenthal, 1988)

A. Absent: The ectoloph is absent.

B. Short: The ectoloph is short.

C. Long: The ectoloph is well-developed.

D. Double: There are two ectolophs.

Mesoloph of the M1 and M2 (from Daams & Freudenthal, 1988)

A. Long: The mesoloph reaches the labial mesocingulum or the labial border of the molar.

B. Medium: The mesoloph exceed the half of the length of the mesosinus.

C. Short: The mesoloph is as long as half of the length of the mesosinus or shorter.

D. Absent: The mesoloph is absent.

Connection of the Ectoloph with the Mesoloph of the M1 and M2 (Modified from Daams & Freudenthal, 1988)

A: The ectoloph is connected with the mesoloph.

B: There is not a connection between the ectoloph and the mesoloph.

C: There is a mesoloph but the ectoloph is absent.

D: There is neither a mesoloph nor an ectoloph.

Metalophule of the M1 (Modified from Daams & Freudenthal, 1988)

Not considered on specimens with strong wear.

A. Isolated: The metalophule is isolated lingually.

B. Anterior: The metalophule points forward and it is connected to the entoloph in front of the hypocone.

C. Transverse: The metalophule is transverse and connected to the hypocone.

D. The metalophule is connected to the posteroloph just behind the hypocone

E. Posterior: The metalophule points backwards reducing the posterosinus.

F. Posterior: The metalophule points backwards more oblique and disappear the posteroloph and the posterosinus (or is very small).

G. Almost double: The posterior metalophule is complete and there is an incomplete second metalophule that is anterior. The latter is formed either, by a crest starting at the entoloph and directed towards the metacone or by the metacone spur.

H. Double: The metalophule is double.

Metalophule of the M2 (Modified from Daams & Freudenthal, 1988 and Oliver & Peláez-Campomanes, 2013)

Not considered on specimens with strong wear.

A. Isolated: The metalophule is isolated lingually.

B. Anterior: The metalophule points forward and it is connected to the entoloph in front of the hypocone.

C. Anterior almost double: The anterior metalophule points forward and is well developed. There is an incomplete posterior metalophule between the posteroloph and the metacone.

D. Transverse: The metalophule is transverse and connected to the hypocone.

E. The metalophule points backwards and it is connected to the posteroloph, just behind the hypocone.

F. The metalophule is more oblique reducing the posterosinus.

G. Posterior almost double: The metalophule points backwards and there is an incomplete second metalophule that is anterior.

H. Double: The metalophule is double.

Metalophule of the M3 (modified from Oliver & Peláez-Campomanes, 2013)

Not considered on specimens with strong wear.

A. The metalophule is absent.

B. The metalophule is connected to the neo-entoloph.

C. The metalophule is connected to the anterior arm of the hypocone.

D. The metalophule is connected to the neo-entoloph (or to the entoloph) and to the protolophule.

E. The metalophule is connected to the anterior arm of the hypocone and the protolophule.

F. The metalophule is connected to the posterior arm of the protocone.

G. The metalophule is connected to the anterior arm of the hypocone, to the protocone and to the second protolophule.

Lower Molars

Anteroconid of the m1 (from Daams & Freudenthal, 1988)

Not considered on specimens with moderate to strong wear.

A. The anteroconid is simple.

B. The anteroconid is slightly subdivided.

C. The anteroconid is 8-shaped with a deep furrow which may rich the basis of the crown.

D. The anteroconid is deeply split.

Antero-lingual cingulid of the m1

A. The antero-lingual cingulid is absent.

B. The cingulid is incipient or have a slight anterior depression.

C. The cingulid is well-developed.

Antero-labial cingulid of the m1 (from Oliver & Peláez-Campomanes, 2013)

A. The antero-labial cingulid is absent.

B. The cingulid is incipient or have a slight anterior depression.

C. The cingulid is well-developed.

Labial Spur of the Anterolophulid of the m1 (from Oliver & Peláez-Campomanes, 2013)

A. The labial spur is absent.

B. There is an incipient labial spur.

C. There is a short (or large) labial spur.

Metalolphulid of the m1 (Modified from Oliver & Peláez-Campomanes, 2013)

A. The metalophulid is isolated labially.

B. The metalophulid points forward even so, it is disconnected to the protoconid.

C. The anterior metalophulid points forward.

D. The anterior metalophulid points forward and there is an incomplete posterior metalophulid.

E. Transverse: The metalophule is transverse and connected to the protoconid.

F. The metalophulid is double.

Mesolophid of the m1 and m2 (from Daams & Freudenthal, 1988)

A. Long: The mesolophid reaches the lingual mesocingulid or the lingual border of the molar.

B. Medium: The mesolophid exceed the half of the length of the mesosinusid.

C. Short: The length of the mesolophid is half of the length of the mesosinusid or shorter.

D. Absent: The mesolophid is absent.

Mesolophid of the m3 (Modified from Daams & Freudenthal, 1988)

A. Absent: The mesolophid is absent.

B. Incipient: The mesolophid is incipient.

C. Present: The mesolophid is well developed.

Ectomesolophid of the m1 (from Oliver & Peláez-Campomanes, 2013)

A. Absent: The ectomesolophid is absent.

B. Incipient: The ectomesolophid is incipient

C. Present: The ectomesolophid is well developed.

Lingual Anterolophid of the m2 and m3 (from Daams & Freudenthal, 1988)

A. Well-developed: The anterolophid reaches the antero-lingual corner of the metaconid.

B. Short: The anterolophid does not reach the antero-lingual corner of the metaconid.

C. Absent: The lingual anterolophid is absent.

The frequency of those character states, in different populations, is used to recognize and differentiate the diverse species of *Megacricetodon*.

The morphological analyses are listed in comparative tables, using character states modified after Daams & Freudenthal (1988), Oliver & Peláez-Campomanes (2013) and Oliver & Peláez-Campomanes (in press). They are included in the different chapters.

For the metrical studies, all the dental elements have been measured (M1, M2, M3 and m1, m2, m3 respectively). Measurements of the teeth have been taken using a Nikon Kosata KK measuring microscope (10x and 15x) and are given in millimeters. The methodology used is after Oliver & Peláez-Campomanes (2013). Length and width represent the maximun antero-posterior and bucco-lingual distances, taken perpendicular to each other (see Figure 2.2.3).

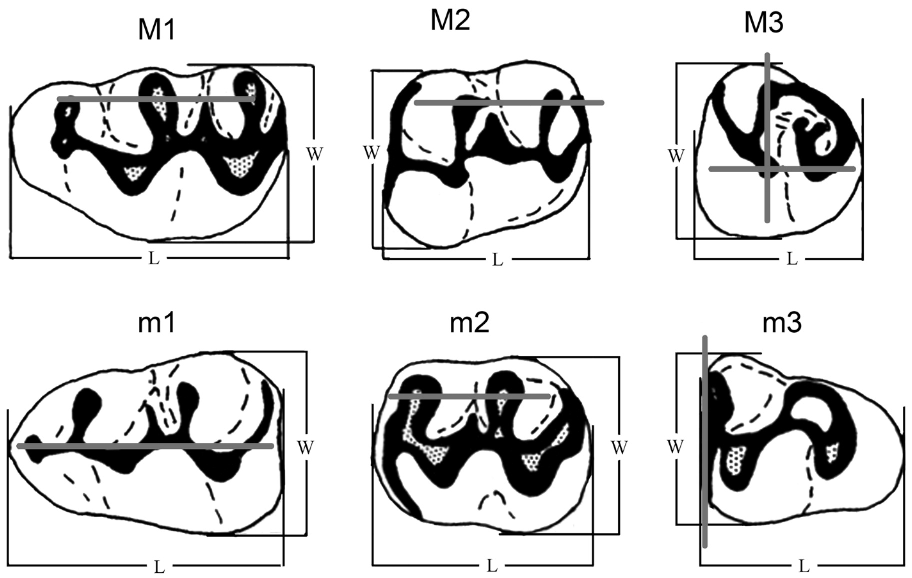


Figure 2.2.3. Measurements of the cheek teeth of *Megacricetodon* in occlusal view (Oliver & Peláez-Campomanes, 2013). The grey bars are the position that should have the tooth in order to measure it correctly. Abbreviations: **L**, length; **W**, width.

The photographs of the occlusal surface of the cheek teeth were made with two different electron microscopes: A low-vacuum ESEM (Fei Inspect-S) and a Scanning Electron Microscope Fei, model Quanta 200 using a large field detector (LFD) or a backscattered electron detector (BSED) (Figure 2.2.4 a,b).

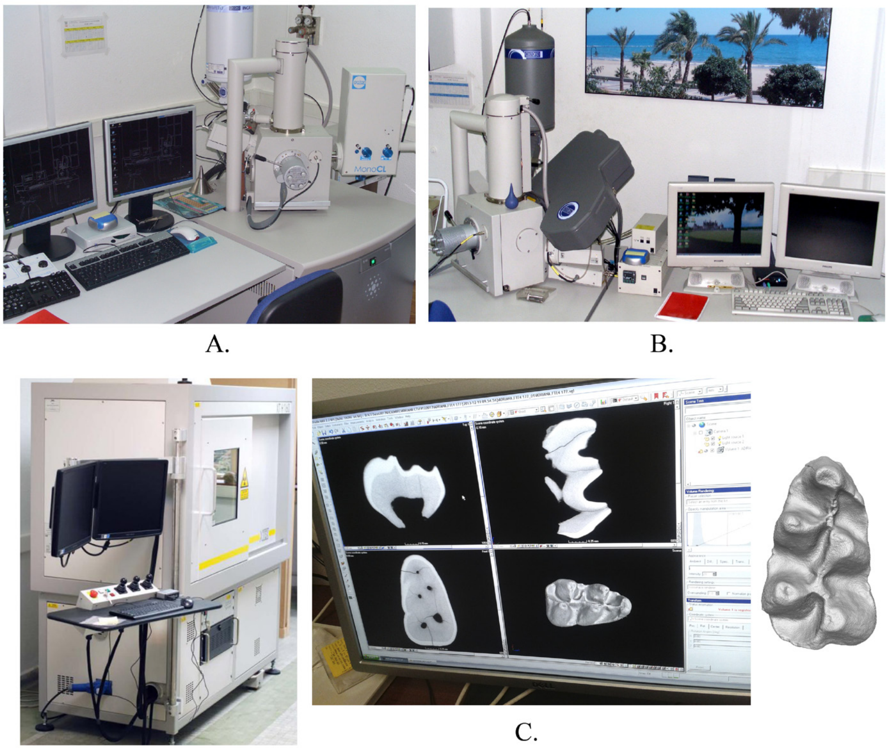


Figure 2.2.4. MNCN Laboratories of non-destructive analytical techniques. A, Inspect-S ESEM of the FEI Company; B, ESEM FEI QUANTA 200 equipped with a large field detector and a backscattered electron detector; C, Micro-CT scanner Nikon XTH 160 and the 3D images obtained.

The 3D images were made using a Micro-CT scanner Nikon XTH 160. For a correct utilization of the CT scan, the teeth should be fixed and vertically positioned. For this purpose the teeth are introduced in a small cylinder of expanded polystyrene, which in turn, is introduced into a plastic cylinder (as shown in Figure 2.254 c). The images are processed using the ImageJ software (Fiji, version 1.48r; Rasband, 1997-2014).

The metrical studies have allowed carried out statistical analysis of the metric variables (mean, standard deviation, standard error, coefficient of variation...) to each of the dental elements. The descriptive statistics were calculated in SPSS version 11.15.1 (SPSS, 2002). To test significant differences among fossil assemblages we carried out analysis of variance (One-Way ANOVA). Previous to the ANOVA, Levene's test was calculated to check for homogeneity of variance. In case of significant ANOVA, post hoc tests were performed (Tukey's significant difference and Hochberg's GT2 when equal variances are assumed; and Games-Howell when not). All analyses were accomplished using exclusively localities with sample sizes larger than four specimens. The statistical analyses were done using SPSS version 11.15.1 (SPSS, 2002).

2.2. REFERENCES

Daams, R., and M. Freudenthal. 1988. Cricetidae (Rodentia) from the type-Aragonian; the genus *Megacricetodon*; pp. 39-132 *in* M. Freudenthal (ed.), Biostratigraphy and paleoecology of the Neogene micromammalian faunas from the Calatayud-Teruel Basin (Spain). Scripta Geologica, Special Issue 1, Leiden.

Daams, R., A. J. van der Meulen, M. A. Álvarez-Sierra, P. Peláez-Campomanes, and W. Krijgsman. 1999. Aragonian stratigraphy reconsidered, and a re-evaluation of the middle Miocene mammal biochronology in Europe. Earth and Planetary Science Letters 165:287-294.

Mein, P. 1975: Biozonation du Néogène Mediterranéen à partir des Mammifères. Paper presented at the VIth Congress of the R.C.M.N.S., Bratislava , Slowakia, 1975.

Oliver, A., and P. Pelaez-Campomanes. 2013. *Megacricetodon vandermeuleni*, sp. nov. (Rodentia, Mammalia), from the Spanish Miocene: a new evolutionary framework for Megacricetodon. Journal of Vertebrate Paleontology 33:943-955.

Oliver, A., and P. Peláez-Campomanes. In press. Evolutionary patterns of early and middle Aragonian (Miocene) of Megacricetodon (Rodentia, Mammalia) from Spain. Palaeontographica Abteilung A.

Oliver, A., and P. Peláez-Campomanes. In press. Early Miocene evolution of the genus *Megacricetodon* in Europe and its palaeobiogeographical implications. Acta Palaeontologica Polonica.

Rasband, W. S. 1997-2014. ImageJ, Bethesda, Maryland, USA.

SPSS. 2002. Statistical Package for the Social Sciences for Windows. SPSS Inc, Chicago.

van Dam, J. A., H. A. Aziz, M. A. A. Sierra, F. J. Hilgen, L. W. V. D. H. Ostende, L. J. Lourens, P. Mein, A. J. van der Meulen, and P. Pelaez-Campomanes. 2006. Long-period astronomical forcing of mammal turnover. Nature 443:687-691.

van der Meulen, A. J., I. García-Paredes, M. A. Álvarez-Sierra, L. W. van den Hoek Ostende, K. Hordijk, A. Oliver, and P. Peláez-Campomanes. 2012. Updated Aragonian biostratigraphy: Small Mammal distribution and its implications for the Miocene European Chronology. Geologica Acta 10:159-179.

3. *Megacricetodon vandermeuleni*

3.1. INTRODUCTION

Since the definition of the sub-genus *Megacricetodon*, almost 50 years ago (Fahlbusch, 1964), numerous species have been defined and phylogenetic hypotheses proposed to relate them. The successive definitions of new species of this genus and the successive revisions of them have promoted the proliferation of lineage definitions with a strong geographic component. For example, Daams & Freudenthal (1988) proposed two *Megacricetodon* lineages for the Spanish material: *M. primitivus-M. ibericus* and *M. minor-M. debruijni*. Aguilar (1995) proposed a new French *Megacricetodon* lineage ("*M. collongensis*"-*M. roussillonensis*) and discussed the different *Megacricetodon* species and lineages among Spain, France and Central Europe. In more recent work (Heissig, 1997; Kälin & Kempf, 2009; Abdul Aziz et al., 2010) the lineage *M.* aff. *collongensis-M. lappi* of mainly Central-European distribution has been used for biochronologic purposes. Lazzari & Aguilar (2007) defined two new species in the French record and proposed one of the most recent phylogenetic hypotheses including taxa from France and Central Europe.

In their recent paper about the formal definition of the small-mammal biozones from the Aragonian type area (Calatayud-Montalbán Basin), Van der Meulen et al., (2012), characterized the local zone Db (middle Aragonian, early MN5, middle Miocene) by the co-occurrence of two *Megacricetodon* species with a clear difference in size: a small-sized *Megacricetodon primitivus* (Freudenthal, 1963) and a large-sized specimen (Daams et al., 1999c) restricted to this local zone and not yet described. Furthermore this zone contains the cricetids *Eumyarion, Democricetodon moralesi*, *Democricetodon franconicus* and *Democricetodon* sp., the latter species also restricted to this zone; five taxa of glirids: *Microdyromys legidensis-koeningswaldi, Prodryomys satus*, *Pseudodryomys ibericus, Armantomys aragonensis* and *Simplomys simplicidens*; and three sciurids: *Heteroxerus* cf. *rubricati, Atlantoxerus blacki* and *Spermophilinus besanus*.

The combination of *M. primitivus* with a larger species was also described by Álvarez Sierra et al. (2006) based on material from La Retama (Loranca Basin). They pointed out the possible taxonomic correspondence between the larger forms from la Retama and the Calatayud-Montalbán Basin. Subsequent studies (Oliver Pérez et al., 2007, Oliver et al., 2009) have applied geometric morphometric analysis to *Megacricetodon* from biozone Db, in order to find morphological differences between both species. *Megacricetodon primitivus* differs morphologically from *M. vandermeuleni* sp. nov. by: 1) an anteroconid in the m1 normally rounded instead of "crescent-shaped" and elongated (Fig. 3.1); 2) the relative position of the main cusps among the teeth; 3) cusp position with regard to the tooth's outline; and 4) the general shape of the outline of the teeth. In this paper we present the

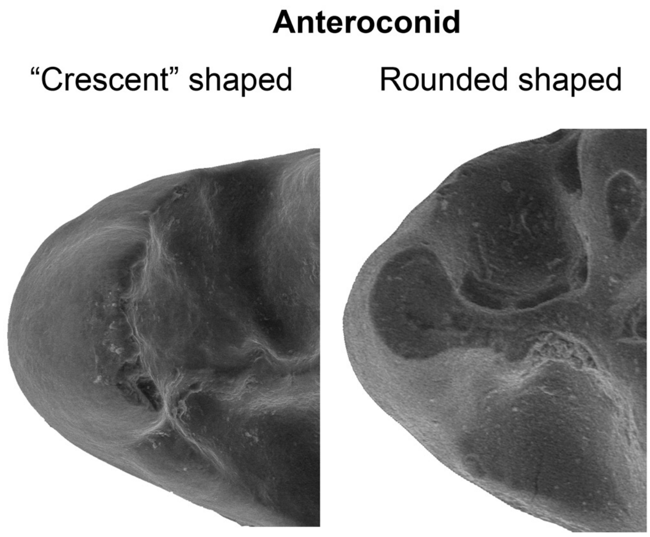


Figure 3.1. Shape of the anteroconids in the lower first molars. To the left, the "crescent"-shape anteroconid, typical of the "*Megacricetodon bavaricus* group". To the right, the rounded shaped, typical of *M. primitivus*.

detailed taxonomic study of this new species of *Megacricetodon*, *M. vandermeuleni* sp. nov., from the Calatayud-Montalbán Basin and the Loranca Basin (Spain, Europe).

During the Spanish Aragonian, several lineages and species of *Megacricetodon* are recognized: the lineage *M.primitivus-M.ibericus*, the lineage *M. minor-M.debruijni*, *M. rafaeli* Daams & Freudenthal, 1988, and *M. lopezae* Garcia-Moreno (in Álvarez-Sierra & García-Moreno, 1986). *Megacricetodon vandermeuleni* sp. nov, cannot be compared with any of these groups because of their different morphological features. There are, however, a group of European species of *Megacricetodon* that, despite differences in size, show similar combination of dental characters, such as the "crescent"-shaped anteroconid and the elongated anterolophulid. This group of species is constituted by: *M. bavaricus* Fahlbusch 1964, *M.* aff. *bavaricus* and *M.* aff. *collongensis* (as considered by Ziegler & Fahlbusch, 1986; Heissig, 1997; Abdul Aziz et al., 2008, 2010), *M. lappi* (Mein, 1958) from Central Europe (Germany and Switzerland); *M. bezianensis* Bulot, 1980, *M. aunayi* Lazzari & Aguilar, 2007 and *M. lappi* (Mein, 1958) from France. After the morphological comparison of all of those taxa with *M. vandermeuleni* sp. nov., we consider that they could form a group of closely related species.

Objectives of the chapter:

- Describe the new species of the local zone Db: *Megacricetodon vandermeuleni*.

- Propose a hypothesis of the phylogenetic relationships among the different taxa of *Megacricetodon*, as well as provide a possible biogeographic framework for their evolution.

3.2. MATERIAL

Megacricetodon vandermeuleni sp. nov. has been recovered from two Spanish basins, the Calatayud-Montalbán Basin and the Loranca Basin. We included five localities of the Calatayud-Montalbán Basin: Fuente Sierra 4, La Col D, Valdemoros 8A, Moratilla 2 and Moratilla 3. And one locality from the Loranca Basin: La Retama.

Other material studied and compared with the Spanish assemblages are: *Megacricetodon robustus* from Nebelbergweg bei Nunningen (Switzerland); *M. bavaricus* from Niederaichbach and Langenmoosen (Germany); *M.*aff. *bavaricus* from Sandelzhausen (Germany); *M.* aff. *collongensis* from Forsthart, Rembach and Rauscheröd 1b, 1c, 1d; *M. aunayi* and *M. "collongensis-gersii"* from Blanquatère 1 (France); *M. gersii* from Sansan (France); *M. lalai* from Châteauredon (France); *M. bourgeoisi* from Suèvres (France); and *M. bezianensis* from Pellecahus, Bézian and La Romieu-Soucaret (France). The material studied by the authors, or based on the literature, is indicated in the corresponding table.

The morphological analyses are listed in comparative tables (see Appendix 3.1, Table 1S-24S).

The specimens described are stored at the Museo Nacional de Ciencias Naturales, CSIC (Madrid, Spain).

3.3. SYSTEMATIC PALAEONTOLOGY

Order RODENTIA Bowdich, 1821

Family MURIDAE Illiger, 1811

Subfamily CRICETODONTINAE Schaub, 1925

Genre *MEGACRICETODON* Fahlbusch, 1964

MEGACRICETODON VANDERMEULENI sp. nov.

(Figs. 3.2 A–T)

Megacricetodon sp. A van der Meulen & Daams, 1992: 230, 231, fig. 1, 240, table 2,242, 249, Appendix 1, table A1.

Megacricetodon sp. Daams et al., 1999c: 126, fig. 1, 127.

Megacricetodon nov. sp. Morales et al., 1999: 257.

Megacricetodon sp. nov. Álvarez Sierra et al., 2006: 413-415, Plate 4, figs. 11-17, table 8, 424.

Megacricetodon sp. Sesé, 2006: 440.

Megacricetodon n. sp. van Dam et al., 2006: 5, Supplementary notes.

Megacricetodon n. sp. 1 van der Meulen et al., 2012: 8.

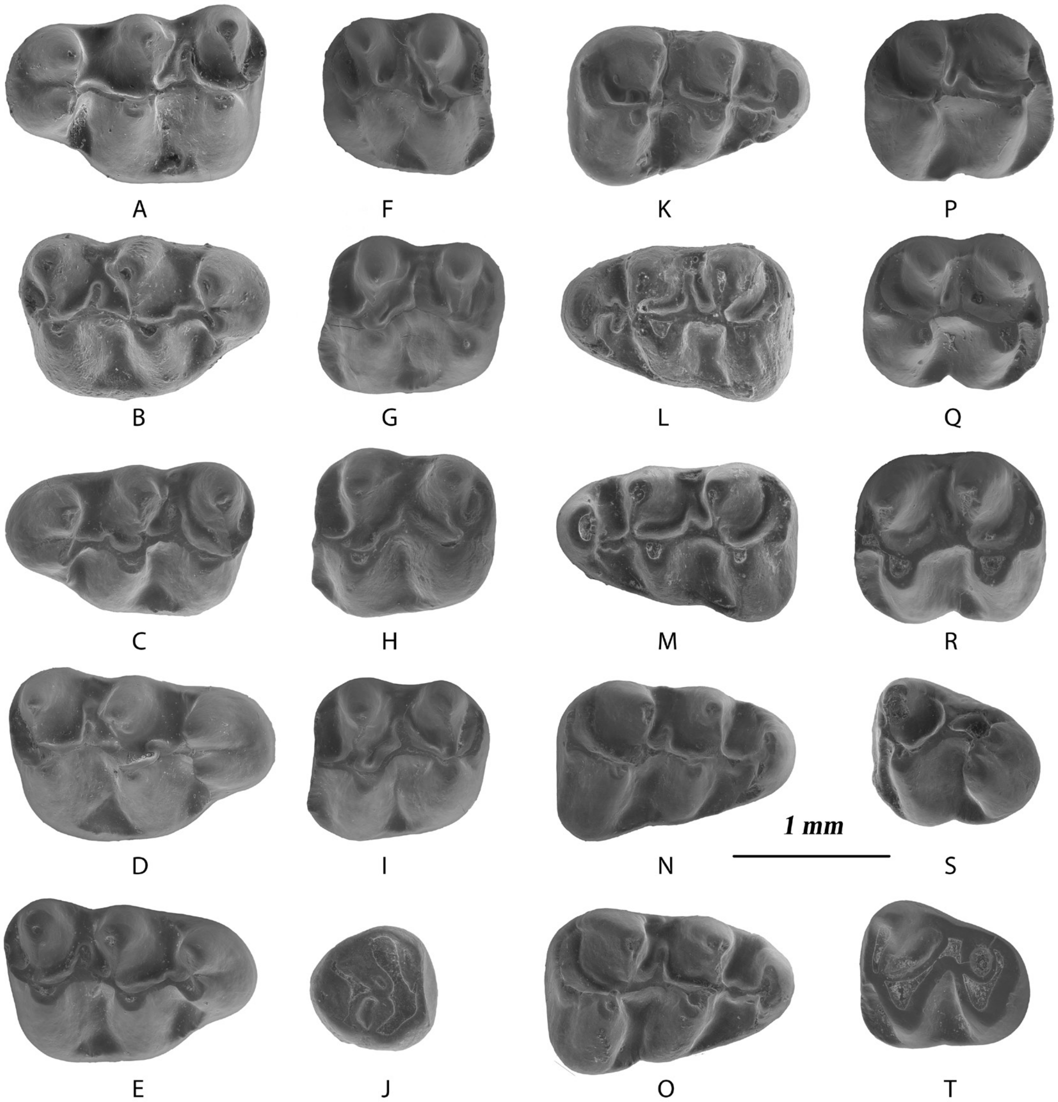


Figure 3.2. *Megacricetodon vandermeuleni* sp. nov. from type locality Fuente Sierra 4. A, FTE4-63 M1 left; B, FTE4-67 M1 right; C, FTE4-156 M1 left; D, FTE4-161 M1 right; E, FTE4-161 M1 right; F, FTE4-72 M2 right; G, FTE4-162 M2 left; H, FTE4-163 M2 left; I, FTE4-164 M2 left; J, FTE4-167 M3 right; K, FTE4-76 m1 right; L, FTE4-169 m1 left; M, FTE4-170 m1 left; N, FTE4-175 m1 right; O, holotype FTE4-177 m1 right; P, FTE4-56 m2 rigth; Q, FTE4-79 m2 rigth; R, FTE4-184 m2 rigth; S, FTE4-188 m3 left; T, FTE4-189 m3 left. All of the teeth are at the same magnification. Scale bar equals 1 mm.

Diagnosis: Large-sized species of *Megacricetodon* (M1 mean length <1,70 mm), with robust and swollen cusps. Elongated first lower molars (long-anterolophulids), anteroconid of m1 (never deeply split) with "crescent"-shape. Mesolophids of short to medium length in m1 and m2.

Differential Diagnosis: According to Peláez-Campomanes & Daams (2002) the different species of *Megacricetodon* can be divided into three different groups of size: small, medium and large. We have updated these groups to included species not considered by those authors, as follows: 1) The small-sized group also includes *M. freudenthali*

Garcia-Moreno (in Álvarez-Sierra & García-Moreno, 1986), *M. minutus* Daxner, 1967, *M. tautavelensis* Lazzari & Aguilar, 2007; 2) The medium-sized group with *M. crisiensis* Radulescu & Samson, 1988; and 3) The large-sized group that includes *M. aunayi* Lazzari & Aguilar, 2007, *M. bezianensis* Bulot, 1980, *M. bourgeoisi* (Schaub, 1925), *M. fahlbuschi* Aguilar et al., 1999, *M. lalai* Aguilar et al., 1999, *M. robustus* Kälin & Engesser, 2001, *M. vandermeuleni* sp. nov., *M. wuae* Aguilar et al., 1999.

Due to the large size of our species, here, we compare it only with the large-sized group.

Megacricetodon vandermeuleni sp. nov. differs from *M. aunayi* Lazzari & Aguilar, 2007, *M. bavaricus* (Fahlbusch, 1964), *M.* aff. *bavaricus* (Fahlbusch, 1964), *M. crusafonti* (Freudenthal, 1963), *M. fahlbuschi* Aguilar et al., 1999, *M. fournasi* Aguilar, 1995, *M. germanicus* Aguilar, 1980, *M. gregarius* (Schaub, 1925), *M. ibericus* (Schaub, 1944), *M. lappi* (Mein, 1958), *M. lemartinelli* Aguilar, 1995, *M. roussillonensis* Aguilar et al., 1986 and *M. wae* Aguilar et al., 1999, by its smaller size.

Megacricetodon robustus Kälin & Engesser, 2001 is similar in size to *M. vandermeuleni* sp. nov.; however, they differ by having the anteroconid always subdivided.

Megacricetodon vandermeuleni sp. nov. has a similar size to *M. lalai* Aguilar, 1999, and *M. gersii* Aguilar, 1980; nevertheless, they differ by the more rounded anteroconid of the m1.

Megacricetodon bezianensis from Bézian, Bulot, 1980, is similarly sized, but differs by having a longer mesolophs(id), and the morphology of the anterocone and the protolophule of the M1.

Megacricetodon vandermeuleni sp. nov. is similar in size to *M. bourgeoisi* (Schaub, 1925); however, the *Megacricetodon* from Suèvres differs by having longer mesolophs, a rounded anteroconid, shorter anterolophulid and a anteriorly directed metalophulid on m1.

We have also compared this taxon to the small-sized *Megacricetodon, M. primitivus*, because they co-occurred during the early Middle Miocene in Spain. *Megacricetodon primitivus* (Freudenthal, 1963) differs by its smaller size, the anteroconid in the m1, normally rounded, the position of the anteroconid that it is near the protoconid and metaconid, and the progressive acquisition, on the M1 of a cingulum that connects the anterocone with the hypocone and runs lingual to the protocone.

			Length					Width				
Element	Sites	Total No.	No.	min	mean	max	σ	No.	min	mean	max	σ
M1	VA8A	42	32	1,52	1,66	1,81	0,07	37	0,97	1,06	1,21	0,06
	MOR3	7	4	1,59	1,67	1,73		5	1,04	1,07	1,11	0,03
	MOR2	23	20	1,53	1,65	1,8	0,06	19	0,99	1,06	1,14	0,04
	FTE4	12	7	1,59	1,64	1,69	0,04	11	1,02	1,05	1,13	0,03
	REM	8	7	1,58	1,68	1,78	0,09	8	0,94	1,05	1,15	0,07
	COL-D	13	9	1,53	1,62	1,73	0,06	10	1,02	1,07	1,11	0,03
M2	VA8A	43	36	1,08	1,16	1,26	0,05	40	0,95	1,04	1,19	0,05
	MOR3	6	5	1,11	1,15	1,18	0,03	5	1,04	1,06	1,11	0,03
	MOR2	18	15	1,1	1,19	1,28	0,06	15	1,01	1,06	1,14	0,04
	FTE4	7	6	1,06	1,12	1,2	0,05	6	1,01	1,06	1,09	0,03
	REM	4	3	1,13	1,17	1,23		2	1,07		1,08	
	COL-D	15	13	1,14	1,19	1,29	0,04	13	1,02	1,06	1,13	0,04
M3	VA8A	5	5	0,76	0,82	0,84	0,03	5	0,82	0,87	0,91	0,03
	MOR3											
	MOR 2	10	6	0,7	0,77	0,84	0,05	6	0,82	0,85	0,88	0,02
	FTE4	1	1		0,77			1		0,78		
	REM	3	3	0,81	0,84	0,89		3	0,85	0,87	0,89	
	COL-D	6	6	0,8	0,85	0,88	0,03	6	0,84	0,86	0,88	0,02
m1	VA8A	39	24	1,39	1,51	1,62	0,06	32	0,85	0,93	1,01	0,04
	MOR3	5	2	1,51		1,61		3	0,9	0,92	0,94	
	MOR2	22	22	1,4	1,55	1,65	0,06	25	0,89	0,95	0,99	0,03
	FTE4	13	12	1,42	1,53	1,61	0,06	13	0,89	0,94	1	0,03
	REM	8	8	1,56	1,62	1,68	0,04	7	0,9	0,97	1	0,03
	COL-D	19	10	1,39	1,51	1,62	0,07	15	0,91	0,96	1,01	0,03
m2	VA8A	38	33	1,1	1,18	1,27	0,04	33	0,97	1,01	1,08	0,03
	MOR3	10	9	1,13	1,23	1,32	0,05	10	0,99	1,04	1,13	0,04
	MOR 2	12	10	1,15	1,21	1,31	0,05	11	0,98	1,02	1,07	0,03
	FTE4	14	10	1,16	1,2	1,27	0,03	12	0,92	0,98	1,01	0,03
	REM	5	4	1,11	1,17	1,22		4	0,97	0,99	1,01	
	COL-D	12	9	1,17	1,23	1,28	0,04	10	0,96	1,01	1,07	0,04
m3	VA8A	12	10	0,99	1,04	1,09	0,03	12	0,81	0,85	0,89	0,02
	MOR3	1	1		1,04			1		0,85		
	MOR 2	22	9	0,95	1	1,07	0,04	10	0,76	0,86	0,93	0,04
	FTE4	3	3	0,96	0,99	1,03		3	0,79	0,82	0,84	
	REM	3	2	0,96		1		2	0,79		0,82	
	COL-D	9	9	0,96	1,02	1,06	0,03	9	0,78	0,81	0,85	0,02

Table 1. Descriptive statistics of *Megacricetodon vandermeuleni* sp. nov. Abbreviations: Total, total number of teeth; N, number of teeth measured; min, minimum; max, maximum; δ, standard deviation.

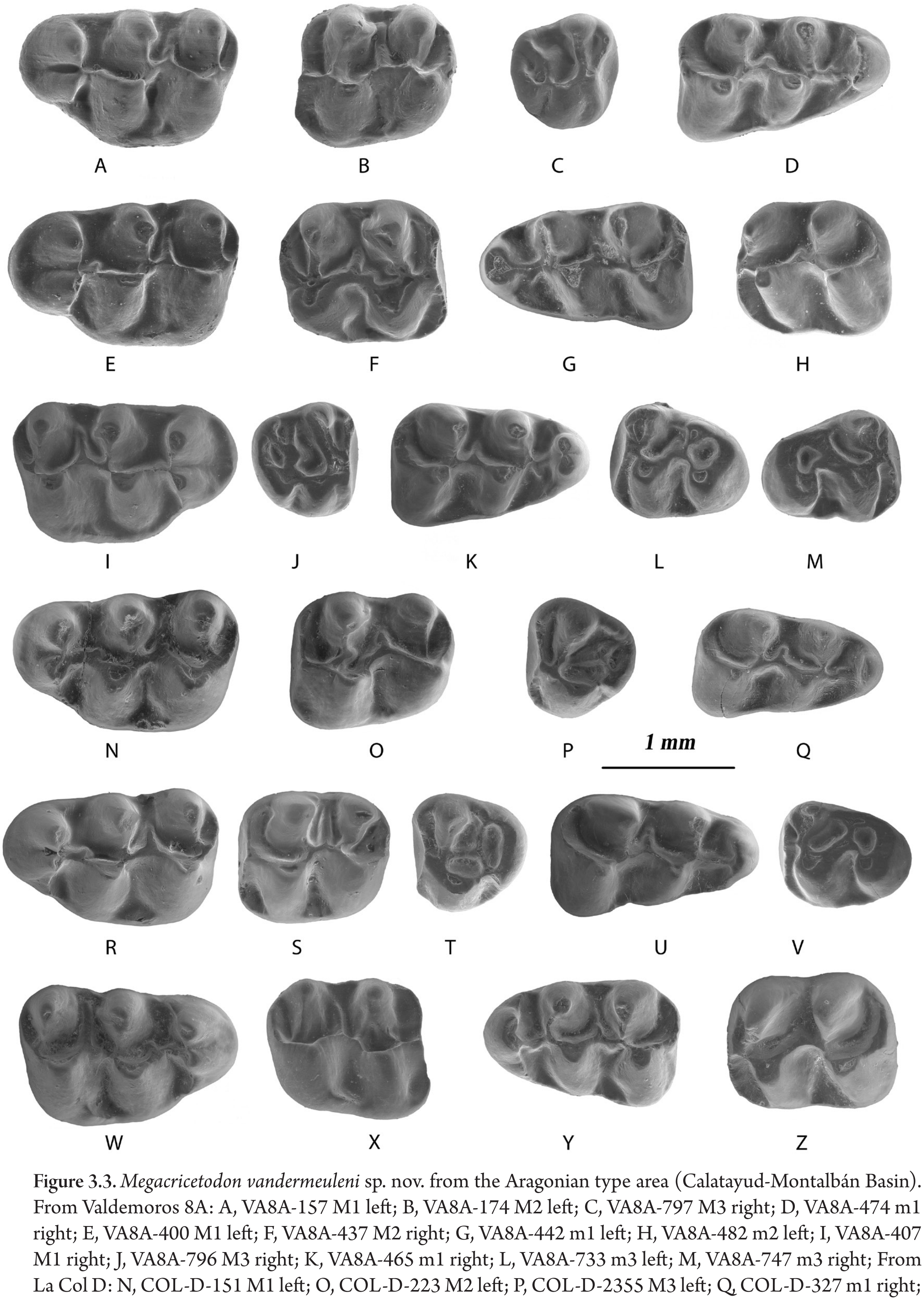


Figure 3.3. *Megacricetodon vandermeuleni* sp. nov. from the Aragonian type area (Calatayud-Montalbán Basin). From Valdemoros 8A: A, VA8A-157 M1 left; B, VA8A-174 M2 left; C, VA8A-797 M3 right; D, VA8A-474 m1 right; E, VA8A-400 M1 left; F, VA8A-437 M2 right; G, VA8A-442 m1 left; H, VA8A-482 m2 left; I, VA8A-407 M1 right; J, VA8A-796 M3 right; K, VA8A-465 m1 right; L, VA8A-733 m3 left; M, VA8A-747 m3 right; From La Col D: N, COL-D-151 M1 left; O, COL-D-223 M2 left; P, COL-D-2355 M3 left; Q, COL-D-327 m1 right; R, COL-D-173 M1 left; S, COL-D-239 M2 left; T, COL-D-2358 M3 left; U, COL-D-339 m1 right; V, COL-D-2917 m3 left; W, COL-D-190 M1 right; X, COL-D-251 M2 right; Y, COL-D-309 m1 left; Z, COL-D-350 m2 left. All of the teeth are at the same magnification. Scale bar equals 1 mm.

Holotype: m1 dext, FTE4-177 (Fig. 3.2 O).

Etymology: Dedicated to our colleague and friend Dr. Albert J. van der Meulen.

Type Locality: Fuente Sierra 4, province of Zaragoza, Calatayud-Montalbán Basin, Spain (local zone Db, MN5, middle Aragonian, middle Miocene).

Paratype: M1: FTE4–36, FTE4–63, FTE4–65, FTE4–67, FTE4–68 FTE4–155 to FTE4–161; M2: FTE4–71, FTE4–72, FTE4–162 to FTE4–166; M3: FTE4–167; m1: FTE4–73 to FTE4–76, FTE4–169 to FTE4–176; m2: FTE4–51 to FTE4–57, FTE4–79, FTE4–180 to FTE4–182, FTE4–184, FTE4–185, FTE4–187; m3: FTE4–188 to FTE4–190.

Other Localities: From the Calatayud-Montalbán Basin: La Col-D (Figs. 6N–Z), Valdemoros 8A (Figs. 6A–M), from the Aragonian type area (Zaragoza); and Moratilla 2 (Figs. 3.4 A–H), Moratilla 3 (Figs. 3.4 I-N), from the Calamocha area (Teruel).

From the Loranca Basin (Cuenca): La Retama (Figs.3. 4 O–R).

Stratigraphical distribution: Local zone Db (middle Aragonian, middle Miocene).

Geographical distribution: Spain.

Measurements: See Table 3.1.

3.4. DESCRIPTION OF THE TYPE MATERIAL

M1: The anterocone is deeply split and the furrow reaches the crown basins in six specimens, while it is slightly subdivided and the furrow is not deep in two out of eight specimens. In four out of eight teeth the labial cone of the anterocone is larger than the lingual; in the remaining four, both present equal size. The anterolophule is mainly connected to the lingual cone of the anterocone (6/7) or between the two lobes of the anterocone (1/7). A short labial spur of the anterolophule is present in two and absent in eight specimens. The protolophule is posterior in seven teeth and posterior almost double in two (Appendix 3.1 Table 1S-5S). The ectoloph is present in 10 specimens (being strong in four of them), and absent in one. A small lingual mesocingulum that connects the protocone with the hypocone is present in seven specimens and it is incipient in the other two. The mesoloph is of intermediate length (7/10) or short (3/10). The metalophule is posterior in seven specimens, anterior in one and connected to the posteroloph just behind the hypocone in one (Appendix 3.1 Table 6S-9S).

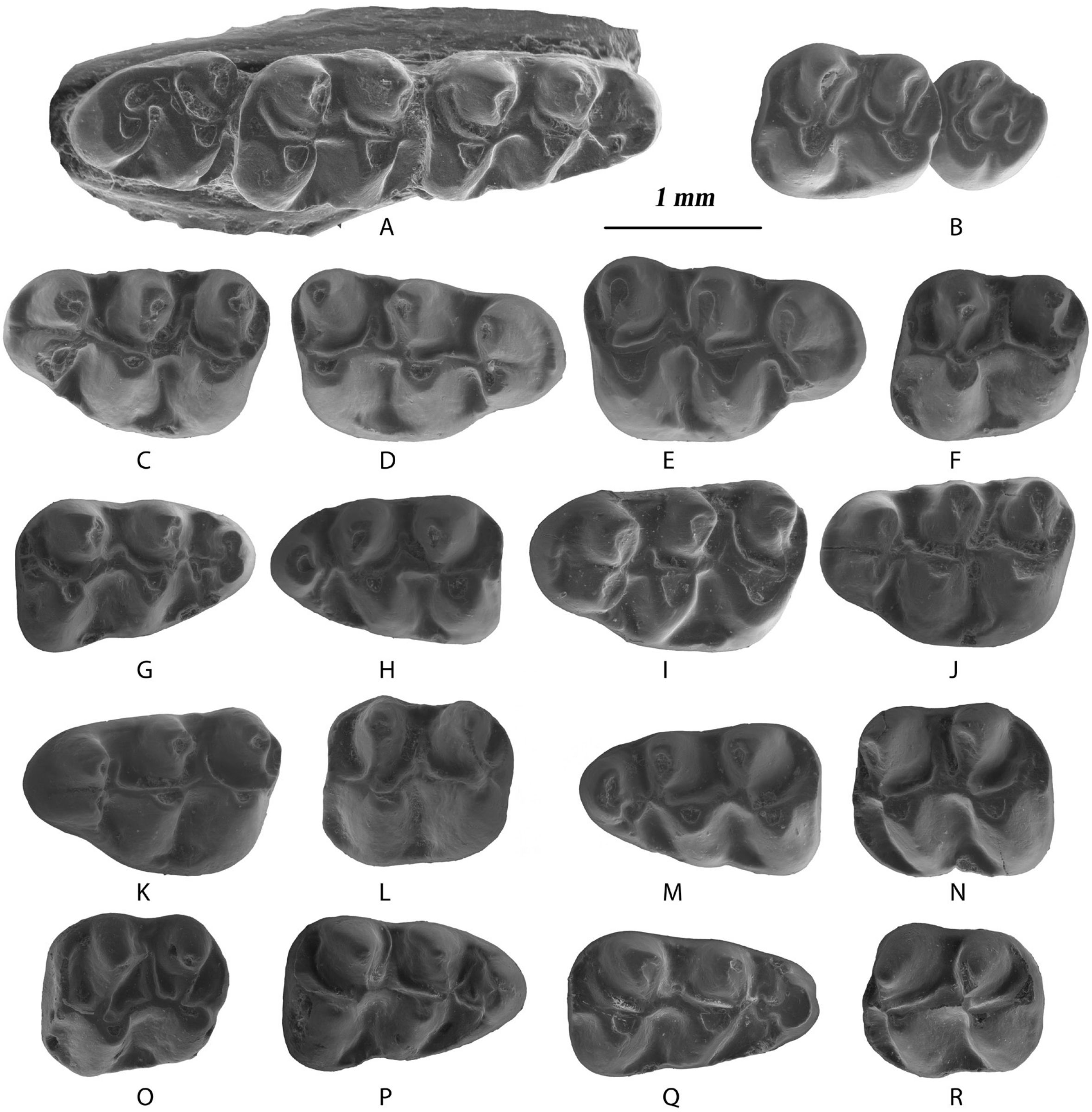


Figure 3.4. *Megacricetodon vandermeuleni* sp. nov. from the Calamocha area (MOR2 and MOR3) and from the Loranca Basin (REM). A, MOR2-5.0 m1-m3 right; B, MOR2-1123 M2-M3 left; C, MOR2-1005 M1 left; D, MOR2-1119 M1 right; E, MOR2-1236 M1 right; F, MOR2-0.5 M2 left; G, MOR2-148 m1 right; H, MOR2-1030 m1 left; I, MOR3-96 M1 left; J, MOR3-97 M1 left; K, MOR3-99 M1 left; L, MOR3-101 M2 left; M, MOR3-80 m1 left; N, MOR3-31 m2 left; O, REM-46 M2 left; P, REM-314 m1 right; Q, REM-319 m1 right; R, REM-370 m2 left. All of the teeth are at the same magnification. Scale bar equals 1 mm.

M2: The protolophule is always directed anteriorly and connected to the anterolophule anterior to the protocone (being almost double in one of them). In five out of seven specimens, the transverse protolophule bends anteriorly before its connection with the protocone (Appendix 3.1 Table 10S). The mesoloph is short in four and medium in three specimens. The metalophule is anterior in five and posterior in one; in one of the former cases the metalophule is transverse but displays a bend before its connection with the hypocone. The ectoloph is present in five out of seven specimens (Appendix 3.1 Table 11S-15S).

M3: Only a heavily-worn specimen is known from the type material. The labial anterolophule connects with the paracone. The paracone is well developed. The posterosinus is elongated and closed.

m1: The anteroconid has an elongated "crescent" shape, being simple in 11 specimens and slightly subdivided in one. The lingual and labial anterolophids are always present. A labial spur of the anterolophulid is present in one specimen, incipient in another and absent in the remaining ten. The lingual spur of the anterolophulid is present in three, incipient in one and absent in eight out of 12 specimens. The labial mesocingulid is always present. The metalophulid is always anteriorly connected to the anterolophulid and in two of them a second connection is almost complete. The mesolophid is short (6/12) or medium (6/12). The hypolophulid is always anterior.

m2: The lingual anterolophulid is short in ten specimens and absent in one. The labial mesocingulid is present in five and absent in one specimen. The lingual mesocingulid is always present. The mesolophid is short (11/12) or intermediate (1/12) in size. The hypolophulid is always anterior.

m3: Two out of three specimens are very worn and thus many of their morphological characters cannot be observed. The lingual anterolophulid is short in the only available specimen. The labial mesocingulid is present but not connected to the hypoconid in two and absent in one. The lingual mesocingulid is present in the three specimens. The mesolophid is always absent.

Comparison with Other Assemblages of M. vandermeuleni *sp. nov.*

Despite assemblages of *Megacricetodon vandermeuleni* sp. nov. from different localities having close similarities in size (Table 3.1 and Fig. 3.5), the type material from Fuente Sierra 4 shows morphological differences when compared with the other assemblages of this species. The anterocone of the specimens from the type locality is less asymmetrical than the rest of the *M. vandermeuleni* sp. nov. specimens from localities in the same basin. The metalophule of M1 is more variable in Fuente Sierra 4 than in the other localities. In contrast, the metalophule of the M2 is always anterior in Fuente Sierra 4, being more variable in the other assemblages. The frequency of protolophules of the M2 that show the bend before the connection with the protocone is higher in the type material. The mesolophid in the m2 from Fuente Sierra 4 is shorter than in the rest of localities (Appendix 3.1 Tables 1S, 9S, 10S, 23S).

In addition, several differences between the type locality and the other assemblages can be pointed out.

The material from La Col D has, in the upper first molars, a higher proportion of specimens with the labial spur of the anterolophule and the ectoloph better developed; it differs by its M2 having protolophule almost double in most of the specimens, and the higher variability of the ectoloph; the lower first molars have higher proportion of anteroconids slightly subdivided, higher frequency of metalophulid with double connexion and ectomesolophids better developed (Appendix 3.1 Tables 4S, 6S, 10S, 12S, 17S, 19S, 21S).

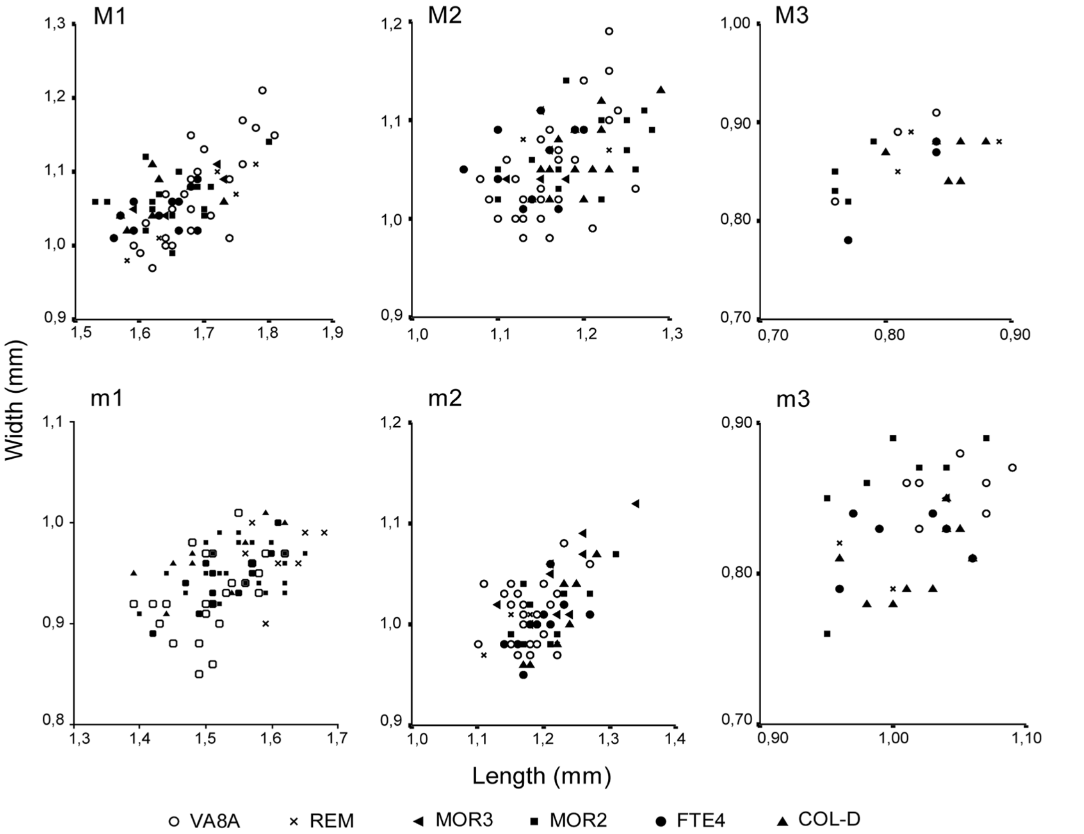


Figure 3.5. Scatterplots with the measurements of *Megacricetodon vandermeuleni* nov. sp. from the type locality (FTE4) and the other assemblages of the zone Db (COL-D, MOR2, MOR3, VA8A and REM).

Moratilla 2 differs from the type locality by its upper first molars with better-split bilobed anterocone and higher frequency of anterolophule starting between the two lobes of the anterocone (see Appendix 3.1 Tables 1S, 3S).

Moratilla 3 shows a higher proportion of M1 with the labial spur of the anterolophule better developed, and shorter mesolophids on m1 (Appendix 3.1 Tables 4S, 20S).

Valdemoros 8A differs from Fuente Sierra 4 by its M1 with better-split bilobed anterocone, a higher frequency of anteroconids slightly subdivided and a higher frequency of a labial spur of the anterolophulid (see Appendix 3.1 Tables 1S, 17S, 18S).

La Retama differs from Fuente Sierra 4 by M1 having a more deeper subdivided anterocone and a higher frequency of anterolophules connected anteriorly between the two lobes of the anterocone; M2 with the protolophule either anterior or transverse and a more-variable connection of the ectoloph with the mesoloph; and its lower first molars having higher proportion of anteroconids slightly subdivided, higher frequency of a labial spur of the anterolophulid and shorter mesolophids.

The upper and lower third molars of *Megacricetodon vandermeuleni* sp. nov. from La Col D are described below to provide a better understanding of the morphological variability of those dental elements, since the material from the type locality is heavily worn and scarce.

M3: The labial anteroloph is always present and extends to the paracone. The lingual anteroloph is absent in two, incipient in two and well developed in one specimen. The paracone is well developed. The metacone is present in two out of four specimens. The hypocone is present in most specimens (4/5). The metalophule is connected to the protolophule and the anterior arm of the hypocone in three specimens, it is connected to the anterior arm of the hypocone in one, and it is connected to the neo-entoloph and the protolophule in one. The mesoloph is absent in three out of five specimens. The second protolophule is always present. The posterior arm of the protocone is absent. In four out of five the neo-entoloph is present, the sinus is always present. The posteroloph is long and connected to the metacone or to the labial mesocingulum in four specimens and isolated labially in one. The posterosinus is always present (being closed in four and open in one).

m3: The labial mesocingulid is absent (2/4), incipient (1/4) or well developed (1/4). The ectostylid is absent in three specimens and present in one. The lingual mesocingulid is always present. The mesolophid is always absent.

3.5. DISCUSSION

According to van der Meulen et al. (2012), the temporal distribution of the species *M. vadermeuleni* sp. nov is approximately 160 Ky, from ~15.84 Ma (COL-D) to ~15.68 Ma (VA8A). Through this time period *M. vandermeuleni* sp. nov. exhibits important changes in dental morphology. The older assemblages (COL-D, FTE4) show slightly subdivided anterocone of M1 and a small lingual mesocingulum that connects only the protocone with the hypocone, whereas, in younger assemblages (MOR2, MOR3, VA8A), the anterocone is more deeply subdivided and has a small platform or a cingulum ridge in front of it, and the lingual mesocingulum connects with the lingual anteroloph around the protocone (Figs. 3.2 D–E; Figs. 3.3 E, I).

Another important change, through the distribution of this species, is in the proportion that represents each of the co-occurring species in the genus *Megacricetodon* (Fig.3.6). In the older localities *M. vandermeuleni* sp. nov. is poorly represented in comparison with the smaller species of *Megacricetodon* (REM and COL-D have a 7.6% and 22.4% % of *M. vandermeuleni* sp. nov. respectively) while, at the end of the local zone Db, *M. vandermeuleni* sp. nov. becomes the dominant species, reaching relative abundances higher than 85% (MOR3 87.9% and VA8A 85%).

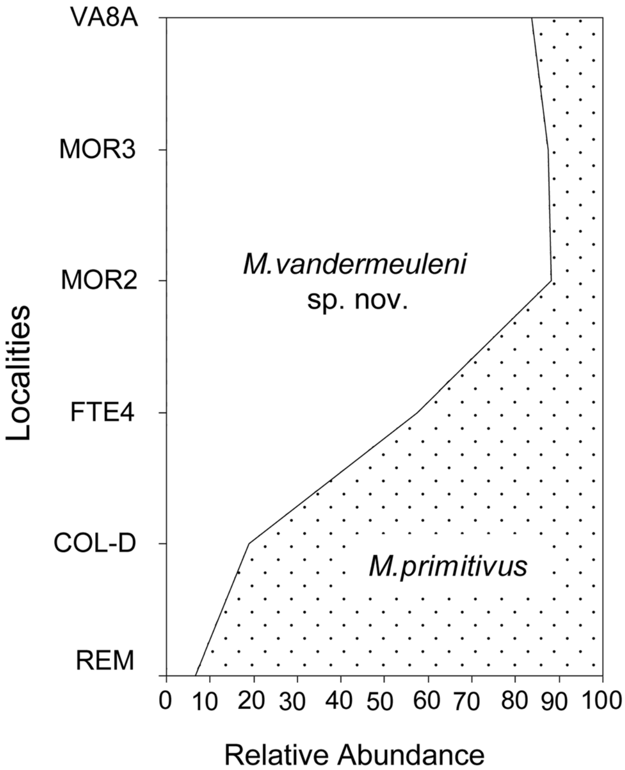


Figure 3.6. Relative abundances between *Megacricetodon vandermeuleni* nov. sp. and *M. primitivus* along biozone Db (middle Aragonian, MN5). The localities of the Calatayud-Montalbán Basin (COL-D, FTE4, MOR2, MOR3 and VA8A) and Loranca Basin (REM) are represented.

La Retama is the only locality outside the Calatayud–Montalbán Basin among the studied material. Some of the metrical (Table 3.1) and morphological differences observed between this *Megacricetodon* assemblage and the one from the type locality could be interpreted as the result of adaptations to different local environmental conditions in the Loranca and Calatayud-Montalbán basins during the middle Aragonian (Álvarez Sierra et al., 2006).

The origin of this new species cannot be related to a speciation event from the Spanish *Megacricetodon primitivus* based on the strong morphological differences between these taxa. It is more probable that it represents a dispersal event of a species with closer relationships to other *Megacricetodon* taxa from Europe.

As has been pointed out in the diagnosis, *M. vandermeuleni* sp. nov. has a combination of morphological characters (the robustness of the teeth, the slender lower first molars, the long anterolophulid, and especially the elongated anteroconid, with a "crescent" shape, of the m1, see Appendix 3.1 Table 17S) that differentiates it from other *Megacricetodon* taxa with similar dental size, such as: 1) *Megacricetodon robustus* from Nebelbergweg, Kälin & Engesser, 2001, which, despite having robust teeth, differs by consistent subdivision of anteroconid, the connection of the anterolophulid with the anteroconid, the lack of mesolophs(ids) and the lack of labial anterocone spur; 2) *Megacricetodon lalai* from the locality of Châteauredon, which differs from the new species by the always simple and rounded morphology of the anteroconid of the m1, and the longer mesolophids (Lalaï, 1986, Aguilar et al., 1999); 3) *Megacricetodon gersii* from Sansan (Baudelot, 1972, Aguilar, 1980), which differs by its rounded anteroconid of the m1, the shorter mesolophs(ids), the morphology of the anterocone, and the larger ectolophs of the M1, the percentage of double protolophule in the M2 and the percentage of ectoloph connected to the mesoloph; and 4) *Megacricetodon bourgeoisi* from Suèvres, which differs in the lower first molar by its always simple and rounded anteroconid, the short-anterololophulid and the anteriorly sloped metalophulid; and in the upper molars, by the longer mesolophs (Bulot, 1988).

There are, however, a group of European species of *Megacricetodon* that, despite differences in size, show a similar combination of dental characters. This group of species is constituted by the following taxa: *M. bavaricus* Fahlbusch 1964, *M.* aff. *bavaricus*, *M.* aff. *collongensis* (as considered by Ziegler & Fahlbusch, 1986; Heissig, 1997; Abdul Aziz et al., 2008, 2010), *M.* aff. *lappi* (as considered by Prieto et al., 2009; Abdul Aziz et al., 2010), *M. lappi* (Mein, 1958), *M. bezianensis* Bulot, 1980, *M. aunayi* Lazzari & Aguilar, 2007, and *M. vandermeuleni* sp. nov. After morphological comparison of these taxa, we consider that they could form a group of closely related species and therefore from here on, we will use the term "*Megacricetodon bavaricus* group" to refer to them.

Despite the similarities of *M. vandermeuleni* sp. nov. to this group of species, there are differences that make us consider the Spanish material as a new taxon. In this way, *Megacricetodon bezianensis* from Bèzian (Bulot, 1980) is different from *M. vandermeuleni* sp. nov. by its longer mesolophs(id), the morphology of the anterocone and the protolophule of the M1. Aguilar (1995) questioned the specific validity of this species, and proposed the synonymy with *M. gersii*. Based on the morphological differences between the type populations of both species, such as the anterocone of the M1, the mesoloph and the ectoloph of the M1 and M2 (Appendix 3.1 Tables 1S-24S), we think that *M. bezianensis* should be considered a valid species different from *M. gersii*, in accordance with Bulot (1980, 1989) and Ginsburg & Bulot (2000).

Megacricetodon aff. *collongensis* from South German Molasse Basin (Rauscheröd 1b+1c, 1d, Rembach and Forsthart in Ziegler & Fahlbusch, 1986), differs by its slightly smaller size, the percentage of the ectoloph in the M1, the larger mesolophs in the M2, the percentage of double protolophules in the M2 and the larger lingual anterolophulid of the m2 (see Appendix 3.1 Tables 6S, 10S, 13S, 22S). Those German *Megacricetodon* assemblages show close dental morphology with *M. bezianensis*. Until further morphological studies on those assemblages are carried out, we maintain the used taxonomical denominations, although our preliminary study indicates that they should probably be assigned to *M. bezianensis*.

Megacricetodon bavaricus from South German Molasse Basin (Langenmoosen and Niederaichbach, in Fahlbusch, 1964), despite its significant larger size, shares particular dental characters with *M. vandermeuleni* sp. nov., such as the morphology of the anteroconid, mesolophs(ids), protolophule M1, M2. However, they differ in the percentage of subdivided anteroconid, the spur on the anterolophulid in the m1 or the slightly subdivided anterocone of the M1 (see Appendix 3.1 Tables 1S-24S). The other two taxa (*M*. aff. *bavaricus* and *M. lappi*) included in the linage defined by Heissig (1990) are much larger than *M. vandermeuleni* nov. sp., and therefore, clearly different from the Spanish form.

Lazzari & Aguilar (2007) described a new species, *M. aunayi* from the French locality of Blanquatère 1. They compared *M. aunayi* with *M. bavaricus* and interpreted these species to have a different anterocone(id) morphology. We do not agree with this interpretation, especially on the m1 (both have "crescent"-shaped anteroconid). In our opinion, *M. aunayi,* might be the same species as *M*. aff. *bavaricus.* They have similar size and similar morphology, such as the elongated anteroconid of the m1, mesolophids of the m1 and m2, protolophule and metalophule of the M1 mainly posterior, and ectoloph of the M1 short or absent.

3.6. PHYLOGENETIC HYPOTHESIS

As we previously commented, numerous authors have proposed different phylogenetic hypotheses (Freudenthal, 1963, 1968; Sesé Benito, 1977; Aguilar, 1980, 1995; Aguilar et al., 1986,1999; Álvarez-Sierra & García-Moreno, 1986; Moreno, 1987; Daams & Freudenthal, 1988; Heissig, 1997; Lazzari & Aguilar, 2007; Kälin & Kempf, 2009; Prieto & Rummel, 2009; Abdul Aziz et al., 2010). In general, most of those phylogenetic hypotheses have a strong geographic component.

Based on the morphological comparison, of the new Spanish taxon described in this work with known *Megacricetodon* taxa from other European basins, we define the "*M. bavaricus* group" and propose a phylogenetic hypothesis for it shown on Figure 3.7, indicating also possible migration events between areas through its distribution. We agree with previous workers that proposed a *M.* aff. *collongensis-M. lappi* lineage (Heissig, 1990, 1997; Kälin et al., 2001; Kälin & Kempf, 2009; Prieto & Rummel, 2009; Abdul Aziz et al., 2010). Our main disagreements are with Aguilar (1995) and Lazzari & Aguilar (2007). The first important difference arises from our interpretation of *M. bezianesis* as a valid species. As discussed before, we reject the synonymy proposed by Aguilar (1995) of *M. bezianensis* from Bézian, La Romieu and other localities from Gers (France) with *M. gersii*, and relate the former species to the "*M. bavaricus* group". The "*M. bavaricus* group" appeared during MN4 in Switzerland, Germany (*M.* aff. *collongensis*) and France (*M. bezianensis*), dispersing through Southwestern Europe during MN5. As discussed previously, those MN 4 species from France and Central Europe show close morphological similarities and therefore they could represent a single taxon.

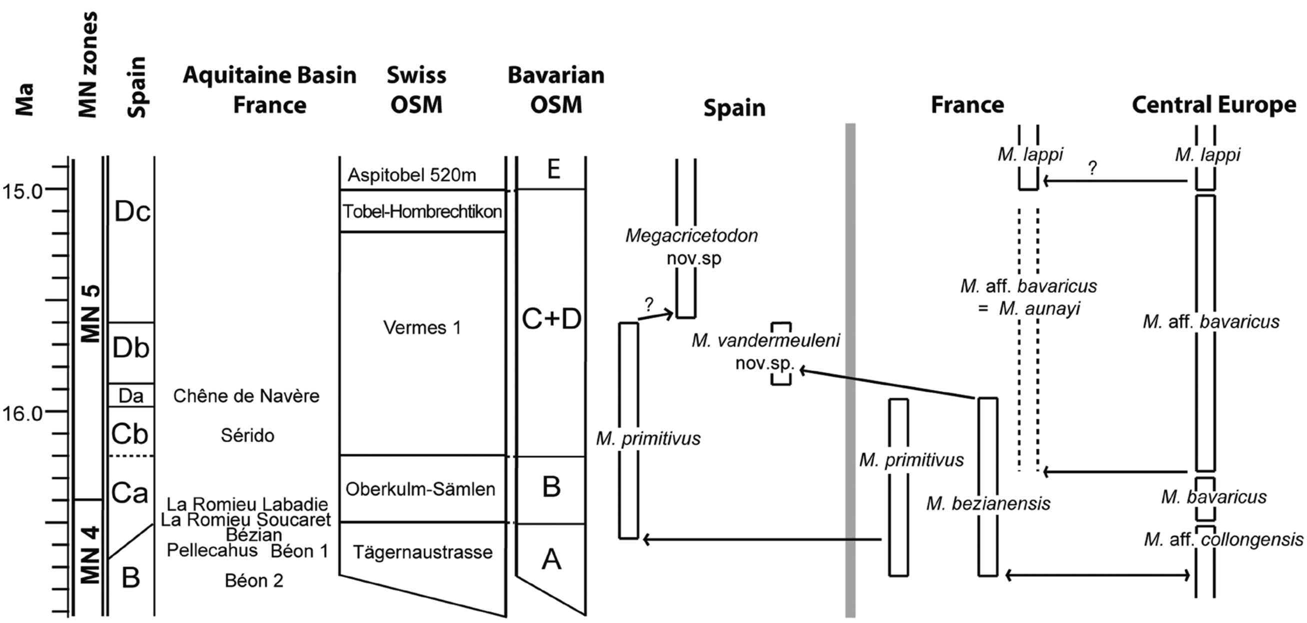


Figure 3.7. Biostratigraphic distribution of selected *Megacricetodon* species from Spain, France, Swiss and South German Molasse Basin, modified from Van der Meulen et al., 2011. The *Megacricetodon* distributions from France are obtained from Antoine et al., 2000; Ginsburg & Bulot, 2000; Bulot et al., 2009. The Central Europe *Megacricetodon* lineages are obtained from Heissig, 1997; Kälin & Kempf, 2009; Abdul Aziz et al., 2010. Arrows indicate possible migrations of species.

Lazzari & Aguilar (2007), based on Aguilar et al., (1999), consider that *M. lalai* is the ancestor of the lineage *M. bavaricus-M.* aff. *bavaricus*. We think that the differences between these species, especially the morphology of the m1 (anteroconid always simple and rounded in *M. lalai*), are strong enough to demonstrate that they are not related, their relationship with the Czech forms from Dolnice 3, Ořechov, Franzensbad and Strakonice, assigned to *M. bavaricus* by Fefjar (1990), being more probable. The latter authors also proposed phylogenetic relationships of *M.* aff. *bavaricus* with their lineage *M. fahlbuschi-M. wuae*. This lineage exhibits an M1 with double anterocone and strong anterior cingulum, and m1 with deeply-split anteroconid and poorly-developed or absent anterolophids. These morphological characters are enough to distinguish them from the "*M. bavaricus* group" and to probably relate them to other European forms such as *M. gregarius* from La Grive or even *M. gersii* from Sansan, although this conclusion must be tested with a further morphological study of the French assemblages, which is outside the scope of this work. Lazzari & Aguilar (2007) allied *M. aunayi* with *M. lappi* because of their similar morphology. Considering that *Megacricetodon aunayi* could be synonyms of *M.* aff. *bavaricus*, this hypothesis would be consistent with those of Heissig, (1990,1997) and Kälin et al., (2001) which united *M.* aff. *bavaricus* and *M. lappi*. In this case *M. aunayi* from Blanquatère 1 would probably represent an immigrant from Central Europe. What cannot be solved with the available information is if the form *M. aunayi/M.* aff. *bavaricus* evolved towards *M. lappi* in both areas or the occurrence of the latter species in France represents a second migration event from Central Europe.

The "*M. bavaricus* group" shows a continuous distribution in Central Europe through the early Aragonian (MN 4 and MN 5) with the lineage *M.* aff. *collongensis-M. lappi. Megacricetodon* aff. *collongensis* during MN 4 (OSM A), and through MN 5 *M. bavaricus* (OSM B), *M.* aff. *bavaricus* (OSM C+D) and finally *M. lappi* (OSM E) (Kälin & Kempf, 2009, Abdul Aziz et al., 2008, 2010). The trends shown by this lineage in Central Europe are towards an increase of size, reduction of mesolophs(ids) and progressive subdivision of the anteroconid. Meanwhile, in France, *Megacricetodon bezianensis* is little variable in its distribution. Neither the size nor the morphology showed changes comparibles to the German "*M. bavaricus* lineage", during MN4 and MN5. In Spain, despite the limited distribution of *M. vandermeuleni* nov. sp., restricted to biozone Db (MN5), several differences in dental morphology have been observed, such as the presence of M1 with a better-developed small cingulum in front of the anterocone, and lingual mesocingulum, in the younger assemblages.

3.7. CONCLUSIONS

We provide a complete description of a new species of *Megacricetodon* from the middle Aragonian of Spain. This large-sized *Megacricetodon* from Calatayud-Montalbán Basin and Loranca Basin is characterized by the morphology of the anteroconid, the elongated anterolophulid, the slender lower first molars, and the robustness of the teeth. *M. vandermeuleni* nov. sp. is restricted to biozone Db and coexisted with the small *M. primitivus*.

We define the "*M. bavaricus* group" inside the genus *Megacricetodon* which include *M.* aff. *collongensis, M. bavaricus, M.* aff. *bavaricus, M. bezianensis, M. lappi* and *M. vandermeuleni* nov. sp. This group would appear during MN4 in France, Switzerland and Germany, dispersing during MN5 through Southwestern Europe.

3.8. REFERENCES

Abdul Aziz, H., M. Böhme, A. Rocholl, J. Prieto, J. R. Wijbrans, V. Bachtadse, and A. Ulbig. 2010. Integrated stratigraphy and 40Ar/39Ar chronology of the Early to Middle Miocene Upper Freshwater Molasse in western Bavaria (Germany). International Journal of Earth Sciences, 99:1859–1886.

Abdul Aziz, H., M. Böhme, A. Rocholl, A. Zwing, J. Prieto, J. R. Wijbrans, K. Heissig, and V. Bachtadse. 2008. Integrated stratigraphy and 40Ar/39Ar chronology of the Early to Middle Miocene Upper Freshwater Molasse in eastern Bavaria (Germany). International Journal of Earth Sciences, 97:115–134.

Aguilar, J. 1980. Nouvelle interpretation de l'evolution du genre *Megacricetodon* au cours du Miocene. Paleovertebrata Volumen Jubilaire R. Lavocat:355–366.

Aguilar, J., G. Clauzon, and J. Michaux. 1999. Nouveaux Cricétidés (Rodentia, Mammalia) dans le Miocène moyen de la région de Digne (Alpes de Haute Provence) Systématique, Biocronologie, Corrélations. Paleontographica 253:1–28.

Aguilar, J. P. 1995. Evolution de la lignée *Megacricetodon collongensis-Megacricetodon rousillonensis* (Cricetidae, Rodentia, Mammalia) au cours du Miocène inférieur et moyen dans le sud de la France. Palaeovertebrata 24:1–45.

Aguilar, J. P., M. Calvet, and J. Michaux. 1986. Découvertes de faunes de micromammifères dans les Pyrénées Orientales (France) de l'Oligocène supérieur au Miocène supérieur; espèces nouvelles et réflexion sur l'étalonnage des échelles continentale et marine. Comptes Rendus de l'Académie des Sciences de Paris Sér. II 303:755–760.

Alcalá, L., A. Alonso-Zarza, M. Álvarez-Sierra, B. Azanza, J. Calvo, J. Cañaveras, J. v. Dam, M. Garcés, W. Krijgsman, A. v. d. Meulen, P. Pélaez-Campomanes, Pérez-González.A, S. Sánchez Moral, R. Sancho, and E. Sanz Rubio. 2000. El registro sedimentario y faunístico de las cuencas de Calatayud-Daroca y Teruel. evolución paleoambiental y paleoclimática durante el neógeno. Revista de la Sociedad Geológica de España 13:323–343.

Álvarez-Sierra, M. A., and E. García-Moreno. 1986. New Gliridae and Cricetidae from the Middle and Upper Miocene of the Duero Basin, Spain. Studia Geologica Salmanticensia, 22:145-189.

Álvarez Sierra, M. A., I. García Paredes, L. W. van den Hoek Ostende, A. J. van der Meulen, P. Peláez-Campomanes, and P. Sevilla. 2006. The Middle Aragonian (Middle Miocene) Micromammals from La Retama (Intermediate Depression, Tagus Basin) Province of Cuenca, Spain. Estudios Geológicos 62:401–428.

Baudelot, S. 1972. Etude des Chiroptères, Insectivores et rongeurs du Miocene de Sansan (Gers). Doctorat d'Etat thesis/dissertation, Thesis University Toulouse, 496:, Toulouse, 1–364. pp.

Bowdich, T. E.1821. An Analysis of the Natural Classification of Mamalia for the Use of Students and Travellers. J. Smith, Paris, 115 pp.

Bruijn, H. d., R. Daams, G. Daxner-Höck, V. Fahlbusch, L. Ginsburg, P. Mein, and J. Morales. 1992. Report of the RCMNS working group on fossil mammals, Reisensburg 1990. Newsletters of Stratigraphy 26:65–118.

Bulot, C. 1980. Nouvelle description de deux espèces du genre *Megacricetodon* (Cricetidae, Rodentia) du Miocène de Bézian (Zone de La Romieu). Bulletin du Museum National d'Histoire Naturelle Section C Sciences de la Terre Paleontologie Geologie Mineralogie, Paris 2(1):3–16.

Bulot, C. 1988. Nouvelle etude des rongeurs et des lagomorphes du Miocene de Suevres (Loir-et-Cher). Bulletin du Museum National d'Histoire Naturelle Section C Sciences de la Terre Paleontologie Geologie Mineralogie, Paris 10.

Bulot, C. 1989. Biostratigraphie des formations continentales de l'Orléanien du Haut-Armagnac (France). Bulletin du Museum National d'Histoire Naturelle, 4e Série, 11(C3):133–139.

Daams, R., and M. Freudenthal. 1988. Cricetidae (Rodentia) from the type Aragonian; the genus *Megacricetodon*; pp. 39–132 in M. Freudenthal (ed.), Biostratigraphy and paleoecology of the Neogene micromammalian faunas from the Calatayud-Teruel Basin (Spain). Scripta Geologica, Special Issue 1, Leiden.

Daams, R., A. J. v. d. Meulen, P. Peláez-Campomanes, and M. A. Álvarez Sierra. 1999a. Trends in rodent assemblages from the Aragonian (Early-Middle Miocene) of the Calatayud-Daroca Basin, Aragón, Spain.; pp. 127–139 in J. Agustí, L. Rook, and P. Andrews (eds.), Hominoid evolution and climatic change in Europe. Cambridge University Press, Cambridge.

Daams, R., A. J. van der Meulen, M. A. Álvarez-Sierra, P. Peláez-Campomanes, and W. Krijgsman. 1999b. Aragonian stratigraphy reconsidered, and a re-evaluation of the Middle Miocene mammal biochronology in Europe. Earth and Planetary Science Letters 165:287–294.

Daams, R., A. J. van der Meulen, M. A. Álvarez-Sierra, P. Peláez-Campomanes, J. P. Calvo, M. A. Alonso Zarza, and W. Krijgsman. 1999c. Stratigraphy and sedimentology of the Aragonian (Early to Middle Miocene) in its type area (North-Central Spain). Newsletters on Stratigraphy 37:103–139.

Daxner, G. 1967. Ein neuer cricetodontide (Rodentia, Mammalia) aus dem Pannon des Wiener Beckens. Annalen des Naturhistorischen Museums in Wien, 71.

Fahlbusch, V. 1964. Die Cricetiden (Mam.) der Oberen Süsswasser-Molasse Bayerns. Bayerische Akademie Wissenschaften. Mathematisch-naturwissenschaftliche Klasse. Munchen 118:1–135.

Fejfar, O. 1990. The Neogene VP sites of Czechoslovakia: A contribution to the neogene terrestric biostratigraphy of Europe based on rodents; pp. 211–236 in E. H. Lindsay, Fahlbusch, V and P. Mein (ed.), European Neogene Mammal Chronology. NATO ASI Series A: Life Sciences. Plenum Press, N.Y.

Freudenthal, M. 1963. Entwicklungsstufen der Miozänen Cricetodontinae (Mam. Rod.). Ph.D. dissertation, Ricks University, Utrecht, 107 pp.

Freudenthal, M. 1968. On the mammalian fauna of the Hipparion beds in the Calatayud-Teruel basin. Part IV: The genus Megacricetodon (Rod.). Proceedings of the Koninklijke Nederlandse Akademie Van Wetenschappen, sér. B, 71(1):57-72.

Freudenthal, M., M. Hugueney, and E. Moissenet. 1994. The genus *Pseudocricetodon* (Cricetidae, Mammalia) in the Upper Oligocene of the province of Teruel (Spain). Scripta Geologica 104:57–114.

Ginsburg, L., and C. Bulot. 2000. Le cadre stratigraphique du site de Sansan. Memoires du Museum National d'Histoire Naturelle, Paris, 183:39–67.

Heissig, K. 1990. The faunal succession of the Bavarian Molasse reconsidered-Correlation of the MN 5 and MN 6 faunas, p. 181–192. *In* E. H. Lindsay, Fahlbusch, V and P. Mein (ed.), European Neogene Mammal Chronology. NATO ASI Series A: Life Sciences. Plenum Press, N.Y.

Heissig, K. 1997. Mammal faunas intermediate between the reference faunas of MN 4 and MN 6 from the Upper Freshwater Molasse of Bavaria. Actes du Congrès BiochroM'97, Montpellier, 21:547–546.

Illiger. 1811. Überblick der Säugthiere nach ihrer Vertheilung über die Welttheile; pp. 39–160 in Abhandlungen de physikalischen Klasse der Königlich-Preussischen Akademie der Wissenschaften. Realschul-Buchhandlung, Berlin.

Kälin, D., and B. Engesser. 2001. Die Jungmiozäne Säugetierfauna vom Nebelbergweg bei Nunningen (Kanton Solothurn, Schweiz). Schweizerische Paläontologische Abhandlungen 121:1–61.

Kälin, D., and O. Kempf. 2009. High-resolution stratigraphy from the continental record of the Middle Miocene Northern Alpine Foreland Basin of Switzerland. Neues Jahrbuch Fur Geologie Und Palaontologie-Abhandlungen, 254(1-2):177–235.

Kälin, D., Weidmann, M., Engesser, B. and Berger, J.-P. 2001. Paléontologie et âge de la Molasse d'eau douce supérieur (OSM) du Jura neuchâtelois. Schweizerische Paläontologische Abhandlungen, 121:65–99.

Lalaï, D. 1986. Nouvelles faunes de rongeurs de la fin du Miocene inférieur en Provence. Implications géologiques et paléogéographiques. Palaeovertebrata 16:77–126.

Lazzari, V., and J. P. Aguilar. 2007. Les *Megacricetodon* du gisement karstique miocène moyen de Blanquatère 1 (Pyrénées-Orientales, Sud de la France): nouvelles espèces, implications biochronologique et phylogénetique. Geobios 40:91–111.

Mein, P. 1958. Les mammifères de la faune sidérolithique du Vieux-Collonges. Nouvelles Archives du Muséum d'Histoire Naturelle de Lyon 5:1–122.

Mein, P. 1975: Biozonation du Néogène Mediterranéen à partir des Mammifères. VIth Congress of the R.C.M.N.S., Bratislava , Slowakia, 1975.

Morales, J., L. Alcalá, M. Hoyos, P. Montoya, M. Nieto, B. Pérez, and D. Soria. 1993. El yacimiento del Aragoniense medio de La Retama (Depresión Intermedia, provincia de Cuenca, España): significado de las faunas con Hispanotherium. Scripta Geologica 103:23–39.

Morales, J., M. Nieto, P. Peláez-Campomanes, D. Soria, M. A. Álvarez Sierra, L. Alcalá, L. Amezua, B. Azanza, E. Cerdeño, R. Daams, S. Fraile, J. Guillem, M. Hoyos, L. Merino, I. de Miguel, R. Monparler, P. Montoya, B. Pérez, M. J. Salesa, and I. M. Sánchez. 1999. Vertebrados continentales del Terciario de la cuenca de Loranca (Provincia de Cuenca); pp. 237–260 in E. Aguirre and I. Rábano (eds.), La huella del pasado: Fósiles de Castilla-La Mancha. Junta de Comunidades de Castilla-La Mancha, Toledo.

Moreno, E. G. 1987. El género *Megacricetodon* (Cricetidae, Rodentia) en el Aragoniense y Vallesiense de la Cuenca del Duero. Relaciones filogenéticas. Coloquios de Paleontología, 41:51-106.

Oliver, A., I. García-Paredes, and P. Pelaez-Campomanes. 2009. A geometric morphometric analysis of *Megacricetodon* (Cricetodontinae, Rodentia, Mammalia) from the Db Biozone, Middle Aragonian. Paleontologia i Evolucio (Memòria especial 3):101–102.

Oliver Pérez, A., P. López Guerrero, M. A. Álvarez Sierra, I. García Paredes, and P. Peláez-Campomanes. 2007: Análisis morfofuncional del género *Megacricetodon* (Cricetidae, Rodentia, Mammalia) de la Biozona Db, Aragoniense medio (Mioceno medio) de la Península Ibérica. XXIII Jornadas de la Sociedad Española de Paleontología, Caravaca de la Cruz, 2007.

Peláez-Campomanes, P., and R. Daams. 2002. Middle Miocene rodents from Pasalar, Anatolia, Turkey. Acta Palaeontologica Polonica 47:125–132.

Prieto, J., and M. Rummel. 2009. Small and medium-sized Cricetidae (Mammalia, Rodentia) from the Middle Miocene fissure filling Petersbuch 68 (southern Germany). Zitteliana Reihe A Mitteilungen der Bayerischen Staatssammlung fuer Palaeontologie und Geologie 48-49.

Prieto, J., M. Böhme, H. Maurer, K. Heissig, and H. Abdul Aziz. 2009. Biostratigraphy and sedimentology of the Fluviatile Untere Serie (Early and Middle Miocene) in the central part of the North Alpine Foreland Basin: implications for palaeoenvironment and climate. International Journal of Earth Sciences 98:1767-1791.

Radulescu, C., and P. Samson. 1988. Les cricetides (Rodentia, Mammalia) du Miocene (Astaracien superieur) de Roumanie. Travaux de l'Institut de Speologie Emile Racovitza 27.

Schaub, S. 1925. Die Hamsterartige Nagetiere des Tertiärs und ihre lebenden Verwandten. Abhandlungen des Schweizerischen paläontologische Gesellschaft. Mémoires de la Société paléontologique suisse 45:1–114.

Schaub, S. 1944. Cricetodontiden der Spanischen Halbinsel. Eclogae Geologicae Helvetiae. Lausanne 37:453–457.

Sesé, C. 2006. Los roedores y lagomorfos del Neógeno de España. Estudios Geológicos 62:429–480.

Sesé Benito, C. 1977. Los Cricétidos (Rodentia, Mammalia) de las fisuras del Mioceno medio de Escobosa de Calatañazor (Soria, España). Trabajos sobre Neógeno-Cuaternario, 8:127-180.

SPSS. 2002. Statistical Package for the Social Sciences for Windows, Rel. 11.5.1. SPSS Inc., Chicago.

van Dam, J. A., H. A. Aziz, M. A. A. Sierra, F. J. Hilgen, L. W. V. D. H. Ostende, L. J. Lourens, P. Mein, A. J. van der Meulen, and P. Pelaez-Campomanes. 2006. Long-period astronomical forcing of mammal turnover. Nature 443:687–691.

van der Meulen, and R. A.J.Daams. 1992. Evolution of Early-Middle Miocene rodent faunas in relation to long-term palaeoenvironment changes. Palaeogeography, Palaeoclimatology, Palaeoecology 93:227–253.

van der Meulen, A.J., I. García-Paredes, M. A. Álvarez-Sierra, L.W. van den Hoek Ostende, K. Hordijk, A. Oliver and P. Peláez-Campomanes. 2012. Updated Aragonian biostratigraphy: Small Mammal distribution and its implications for the Miocene European Chronology. Geologica Acta. Doi: 101344/105000001710.

van der Meulen, A. J., I. García-Paredes, M. Á. Álvarez-Sierra, L. W. v. d. H. Ostende, K. Hordijk, A. Oliver, P. López-Guerrero, V. Hernández-Ballarín, and P. Peláez-Campomanes. 2011. Biostratigraphy or biochronology? Lessons from the Early and Middle Miocene small Mammal Events in Europe. Geobios, 44(2-3):309-321.

Ziegler, R., and V. Fahlbusch. 1986. Kleinsäuger-Faunen aus der basalen Oberen Süsswasser-Molasse Niederbayerns. Zitteliana 14:3–58.

APPENDIX 3.1

DISTRIBUTION OF CHARACTER STATES

The data from *M. bezianensis* from Bézian and *M. bourgeoisi* from Suèvres are described by Bulot, 1980 and Bulot, 1988, respectively.

Table 1. Anterocone M1

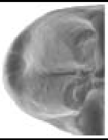
Localities						N
Niederaichbach (*M.bavaricus*)	2 (14%)	6 (43%)	3 (21%)	3 (21%)		14
Langenmoosen (*M. bavaricus*)			20 (69%)	7 (24%)	2 (7%)	29
Forsthart (*M. aff. collongensis)*	1 (10%)		5 (50%)	4 (40%)		10
Rembach (*M. aff. collongensis*)			3 (43%)	4 (57%)		7
Rauscheröd 1b, 1c, 1d (*M. aff. collongensis*)	2 (9%)		11 (50%)	9 (41%)		22
Sandelzhausen (*M.* aff. *bavaricus)*				7 (100%)		7
Blanquatère 1 (*M. aunayi*)	5 (9%)		16 (30%)	31 (58%)	1 (2%)	53
Blanquatère 1 (*M. "collongensis-gersii"*)	4 (6%)		7 (10%)	47 (70%)	9 (13%)	67
Sansan (*M.gersii*)			1 (10%)	8 (80%)	1 (10%)	10
Châteauredon (*M.lalaï*)	1 (3%)	6 (21%)	13 (45%)	9 (31%)		29
Suèvres (*M.bourgeoisi*)	2 (33%)			3 (50%)	1 (17%)	6
La Romieu-Soucaret (*M. bezianensis*)			10 (67%)	5 (33%)		15
Bézian (*M. bezianensis*)	39 (94%)		2 (5%)	22 (35%)		63
Valdemoros 8A	2 (6%)	6 (18%)	5 (15%)	19 (58%)	1 (3%)	33
Moratilla 3		1 (20%)	4 (80%)			5
Moratilla 2	1 (6%)	3 (19%)	3 (19%)	9 (56%)		16
Fuente Sierra 4	2 (25%)		6 (75%)			8
La Retama		1 (14%)	2 (29%)	1 (14%)	3 (43%)	7
La Col-D	2 (29%)		5 (71%)			7

Table 2. Symmetry of the Anterocone M1

Localities				N
Niederaichbach (*M.bavaricus*)	1 (17%)	5 (83%)		6
Langenmoosen (*M. bavaricus*)	1 (3%)	35 (97%)		36
Forsthart (*M. aff. collongensis)*		15 (100%)		15
Rembach (*M. aff. collongensis*)		9 (100%)		9
Rauscheröd 1b, 1c, 1d (*M. aff. collongensis*)		21 (100%)		21
Sandelzhausen (*M.* aff. *bavaricus)*		7 (100%)		7
Blanquatère 1 (*M. aunayi*)	6 (10%)	53 (90%)		59
Blanquatère 1 (*M. "collongensis-gersii"*)	9 (12%)	64 (88%)		73
Sansan (*M.gersii*)	4 (36%)	7 (64%)		11
Châteauredon (*M.lalaï*)	7 (19%)	28 (78%)	1 (3%)	36
Suèvres (*M.bourgeoisi*)		(100%)		
La Romieu-Soucaret (*M. bezianensis*)	1 (6%)	15 (88%)	1 (6%)	17
Bézian (*M. bezianensis*)		63 (100%)		63
Valdemoros 8A	4 (11%)	33 (89%)		37
Moratilla 3		5 (100%)		5
Moratilla 2	5 (28%)	13 (72%)		18
Fuente Sierra 4	4 (50%)	4 (50%)		8
La Retama	1 (14%)	6 (86%)		7
La Col-D		7 (100%)		7

Table 3. Anterolophule M1

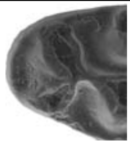
Localities				N
Blanquatère 1 (*M. aunayi*)	4 (6%)	66 (94%)		70
Blanquatère 1 (*M. "collongensis-gersii"*)	39 (49%)	38 (48%)	2 (3%)	79
Sansan (*M.gersii*)	5 (71%)	2 (29%)		7
La Romieu-Soucaret (*M. bezianensis*)	6 (35%)	11 (65%)		17
Bézian (*M. bezianensis*)		63 (100%)		63
Valdemoros 8A	12 (32%)	26 (68%)		38
Moratilla 3		4 (100%)		4
Moratilla 2	8 (42%)	11 (58%)		19
Fuente Sierra 4	1 (14%)	6 (86%)		7
La Retama	4 (57%)	3 (43%)		7
La Col-D	1 (10%)	9 (90%)		10

Table 4. Labial Spur of the Anterolophule M1

Localities				N
Niederaichbach (*M.bavaricus*)	3 (50%)		3 (50%)	6
Langenmoosen (*M. bavaricus*)	11 (28%)	4 (10%)	24 (62%)	39
Forsthart (*M.* aff. *collongensis)*	7 (50%)	1 (7%)	6 (43%)	14
Rembach (*M*. aff. *collongensis*)	6 (60%)	1 (10%)	3 (30%)	10
Rauscheröd 1b, 1c, 1d (*M*. aff. *collongensis*)	7 (27%)	1 (4%)	18 (69%)	26
Nebelbergweg bei Nunningen (*M. robustus*)			5 (100%)	5
Sandelzhausen (*M.* aff. *bavaricus)*			7 (100%)	7
Blanquatère 1 (*M. aunayi*)	15 (22%)	1 (1%)	52 (76%)	68
Blanquatère 1 (*M. "collongensis-gersii"*)	27 (34%)	3 (4%)	50 (63%)	80
Sansan (*M.gersii*)	1 (10%)	1 (10%)	8 (80%)	10
Châteauredon (*M.lalaï*)	7 (18%)	3 (8%)	29 (74%)	39
La Romieu-Soucaret (*M. bezianensis*)	6 (38%)	1 (6%)	9 (56%)	16
Bézian (*M. bezianensis*)	10 (16%)		53 (84%)	63
Valdemoros 8A	11 (26%)	5 (12%)	26 (62%)	42
Moratilla 3	4 (80%)		1 (20%)	5
Moratilla 2	2 (10%)	2 (10%)	16 (80%)	20
Fuente Sierra 4	2 (20%)		8 (80%)	10
La Retama	2 (25%)		6 (75%)	8
La Col-D	7 (58%)		5 (42%)	12

Table 5S. Protolophule of the M1

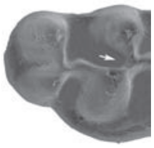
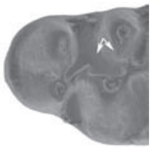
Localities				N
Niederaichbach (*M.bavaricus*)	4 (80%)	1 (20%)		5
Langenmoosen (*M. bavaricus*)	28 (78%)	7 (19%)	1 (3%)	36
Forsthart (*M.* aff. *collongensis)*	11 (79%)	3 (21%)		14
Rembach (*M*. aff. *collongensis*)	8 (80%)	1 (10%)	1 (10%)	10
Rauscheröd 1b, 1c, 1d (*M*. aff. *collongensis*)	24 (92%)	2 (8%)		26
Sandelzhausen (*M.* aff. *bavaricus)*	6 (86%)		1 (14%)	7
Blanquatère 1 (*M. aunayi*)	52 (84%)	6 (10%)	4 (6%)	62
Blanquatère 1 (*M. "collongensis-gersii"*)	51 (69%)	10 (14%)	13 (18%)	74
Sansan (*M.gersii*)	10 (100%)			10
Suèvres (*M.bourgeoisi*)	(100%)			
Châteauredon (*M.lalaï*)	33 (87%)	5 (13%)		38
La Romieu-Soucaret (*M. bezianensis*)	10 (77%)	3 (23%)		13
Bézian (*M. bezianensis*)	63 (97%)	2 (3%)		65
Valdemoros 8A	32 (97%)	1 (3%)		33
Moratilla 3	3 (75%)		1 (25%)	4
Moratilla 2	14 (93%)	1 (7%)		15
Fuente Sierra 4	7 (78%)	2 (22%)		9
La Retama	8 (89%)	1 (11%)		9
La Col-D	6 (50%)	5 (42%)	1 (8%)	12

Table 6S. Ectoloph M1

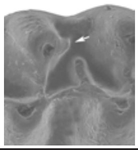
Localities				N
Niederaichbach (*M.bavaricus*)		5 (100%)		5
Langenmoosen (*M. bavaricus*)	13 (34%)	25 (66%)		38
Forsthart (*M.* aff. *collongensis)*	1 (7%)	13 (87%)	1 (7%)	15
Rembach (*M*. aff. *collongensis*)	1 (10%)	9 (90%)		10
Rauscheröd 1b, 1c, 1d (*M*. aff. *collongensis*)	2 (7%)	24 (89%)	1 (4%)	27
Sandelzhausen (*M.* aff. *bavaricus)*	6 (86%)	1 (14%)		7
Blanquatère 1 (*M. aunayi*)	39 (56%)	31 (44%)		70
Blanquatère 1 (*M. "collongensis-gersii"*)	38 (48%)	42 (53%)		80
Sansan (*M.gersii*)	2 (18%)	9 (82%)		11
Châteauredon (*M.lalaï*)	4 (11%)	30 (79%)	4 (11%)	38
La Romieu-Soucaret (*M. bezianensis*)	5 (31%)	11 (69%)		16
Bézian (*M. bezianensis*)	22 (35%)	41 (65%)		63
Valdemoros 8A	13 (35%)	24 (65%)		37
Moratilla 3	2 (50%)	2 (50%)		4
Moratilla 2	7 (41%)	9 (53%)	1 (6%)	17
Fuente Sierra 4	1 (9%)	6 (55%)	4 (36%)	11
La Retama	4 (40%)	4 (40%)	2 (20%)	10
La Col-D	2 (18%)	8 (73%)	1 (9%)	11

Table 7S. Mesoloph M1

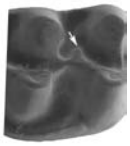
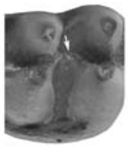
Localities					N
Niederaichbach (*M.bavaricus*)		2 (40%)	3 (60%)		5
Langenmoosen (*M. bavaricus*)	1 (3%)	29 (76%)	8 (21%)		38
Forsthart (*M.* aff. *collongensis)*	1 (7%)	7 (47%)	7 (47%)		15
Rembach (*M*. aff. *collongensis*)		8 (80%)	2 (20%)		10
Rauscheröd 1b, 1c, 1d (*M*. aff. *collongensis*)		18 (67%)	8 (30%)	1 (4%)	27
Nebelbergweg bei Nunningen (*M. robustus*)		1 (20%)	3 (60%)	1 (20%)	5
Sandelzhausen (*M.* aff. *bavaricus)*	1 (14%)	5 (71%)	1 (14%)		7
Blanquatère 1 (*M. aunayi*)		26 (37%)	41 (59%)	3 (4%)	70
Blanquatère 1 (*M. "collongensis-gersii"*)		47 (60%)	31 (40%)		78
Sansan (*M.gersii*)		1 (9%)	10 (91%)		11
Châteauredon (*M.lalaï*)		23 (59%)	16 (41%)		39
Suèvres (*M.bourgeoisi*)	7 (88%)		1 (13%)		8
La Romieu-Soucaret (*M. bezianensis*)		8 (47%)	9 (53%)		17
Bézian (*M. bezianensis*)		56 (89%)	7 (11%)		63
Valdemoros 8A		21 (51%)	20 (49%)		41
Moratilla 3		3 (60%)	2 (40%)		5
Moratilla 2		15 (71%)	6 (29%)		21
Fuente Sierra 4		7 (70%)	3 (30%)		10
La Retama		6 (60%)	4 (40%)		10
La Col-D		5 (38%)	8 (62%)		13

Table 8S. Connection Mesoloph-Ectoloph M1

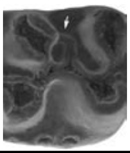
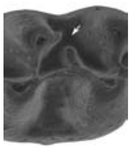
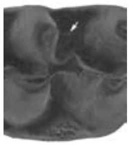
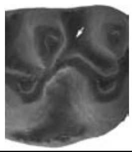
Localities					N
Niederaichbach (*M.bavaricus*)	1 (20%)	4 (80%)			5
Langenmoosen (*M. bavaricus*)	1 (3%)	23 (62%)	13 (35%)		37
Forsthart (*M.* aff. *collongensis)*	1 (7%)	12 (86%)	1 (7%)		14
Rembach (*M*. aff. *collongensis*)		9 (90%)	1 (10%)		10
Rauscheröd 1b, 1c, 1d (*M*. aff. *collongensis*)	4 (16%)	18 (72%)	2 (8%)	1 (4%)	25
Nebelbergweg bei Nunningen (*M. robustus*)		3 (60%)	2 (40%)		5
Sandelzhausen (*M.* aff. *bavaricus)*		1 (14%)	6 (86%)		7
Blanquatère 1 (*M. aunayi*)	2 (3%)	30 (43%)	34 (49%)	3 (4%)	69
Blanquatère 1 (*M. "collongensis-gersii"*)		41 (52%)	38 (48%)		79
Sansan (*M.gersii*)	3 (27%)	6 (55%)	2 (18%)		11
Châteauredon (*M.lalaï*)		35 (92%)	3 (8%)		38
La Romieu-Soucaret (*M. bezianensis*)		11 (69%)	5 (31%)		16
Bézian (*M. bezianensis*)		41 (65%)	22 (35%)		63
Valdemoros 8A		23 (64%)	13 (36%)		36
Moratilla 3		2 (50%)	2 (50%)		4
Moratilla 2	1 (6%)	9 (53%)	7 (41%)		17
Fuente Sierra 4	2 (18%)	8 (73%)	1 (9%)		11
La Retama	1 (10%)	5 (50%)	4 (40%)		10
La Col-D		8 (80%)	2 (20%)		10

Table 9S. Metalophule M1

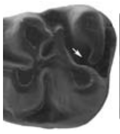
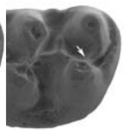
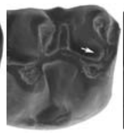
Localities									N
Niederaichbach (*M. bavaricus*)					4 (80%)	1 (20%)			5
Langenmoosen (*M. bavaricus*)					22 (76%)	4 (14%)	1 (3%)	2 (7%)	29
Forsthart (*M.* aff. *collongensis*)			1 (10%)		9 (90%)				10
Rembach (*M* aff. *collongensis*)		2 (22%)			7 (78%)				9
Rauscheröd 1b, 1c, 1d (*M* aff. *collongensis*)	1 (5%)		3 (14%)	2 (10%)	15 (71%)				21
Sandelzhausen (*M.* aff. *bavaricus*)					7 (100%)				7
Blanquatère 1 (*M. aunayi*)	1 (2%)		3 (5%)	8 (14%)	47 (80%)				59
Blanquatère 1 (*M. "collongensis-gersii"*)				7 (11%)	47 (77%)	5 (8%)		2 (3%)	61
Sansan (*M. gersii*)				5 (56%)	4 (44%)				9
Châteauredon (*M. lalai*)			1 (3%)	2 (6%)	33 (92%)				36
Suèvres (*M .bourgeoisi*)			2 (25%)		6 (75%)				8
La Romieu-Soucaret (*M. bezianensis*)			1 (8%)		12 (92%)				13
Bézian (*M. bezianensis*)		1 (2%)	2 (3%)	1 (2%)	59 (94%)				63
Valdemoros 8A				1 (4%)	23 (88%)	1 (4%)		1 (4%)	26
Moratilla 3					3 (100%)				3
Moratilla 2				1 (8%)	11 (92%)				12
Fuente Sierra 4		1 (11%)		1 (11%)	7 (78%)				9
La Retama					7 (100%)				7
La Col-D					10 (100%)				10

Table 10S. Protolophule M2

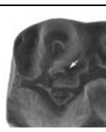
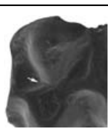
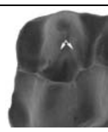
Localities						N
Niederaichbach (*M.bavaricus*)	1 (100%)					1
Langenmoosen (*M. bavaricus*)	11 (48%)	8 (35%)	1 (4%)	3 (13%)		23
Forsthart (*M.* aff. *collongensis)*	8 (73%)			3 (27%)		11
Rembach (*M*. aff. *collongensis*)	2 (20%)	7 (70%)		1 (10%)		10
Rauscheröd 1b, 1c, 1d (*M*. aff. *collongensis*)	8 (42%)	8 (42%)		3 (16%)		19
Sandelzhausen (*M.* aff. *bavaricus)*	8 (80%)		2 (20%)			10
Sansan (*M.gersii*)	3 (60%)			2 (40%)		5
Suèvres (*M.bourgeoisi*)	2 (67%)	1 (33%)				3
Châteauredon (*M.lalaï*)	13 (27%)	21 (44%)		14 (29%)		48
La Romieu-Soucaret (*M. bezianensis*)	9 (56%)	5 (31%)	1 (6%)	1 (6%)		16
Bézian (*M. bezianensis*)	48 (73%)	12 (18%)	1 (2%)	5 (8%)		66
Pellecahus (*M. bezianensis*)	2 (100%)					2
Valdemoros 8A	22 (61%)	9 (25%)	4 (11%)	1 (3%)		36
Moratilla 3	2 (100%)					2
Moratilla 2	14 (78%)	1 (6%)	2 (11%)	1 (6%)		18
Fuente Sierra 4	6 (86%)	1 (14%)				7
La Retama	1 (50%)		1 (50%)			2
La Col-D	2 (15%)	9 (69%)		1 (8%)	1 (8%)	13

Table 11S. Anterior Protolophule M2

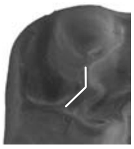
Localities				N
Langenmoosen (*M. bavaricus*)	20 (95%)	1 (5%)		21
Rembach (*M*. aff. *collongensis*)	8 (89%)	1 (11%)		9
Rauscheröd 1b, 1c, 1d (*M*. aff. *collongensis*)	15 (94%)	1 (6%)		16
Sansan (*M.gersii*)	3 (100%)			3
Châteauredon (*M.lalaï*)	13 (100%)			13
La Romieu-Soucaret (*M. bezianensis*)	8 (89%)		1 (11%)	9
Valdemoros 8A	22 (73%)	6 (20%)	2 (7%)	30
Moratilla 3	1 (50%)	1 (50%)		2
Moratilla 2	12 (80%)	2 (13%)	1 (7%)	15
Fuente Sierra 4	2 (29%)	5 (71%)		7
La Retama	1 100%			1
La Col-D	9 (82%)	2 (18%)		11

Table 12S. Ectoloph M2

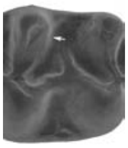
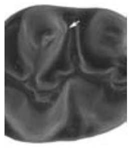
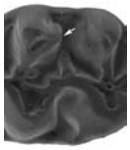
Localities				N
Langenmoosen (*M. bavaricus*)	1 (4%)	20 (74%)	6 (22%)	27
Forsthart (*M.* aff. *collongensis)*	1 (8%)	8 (67%)	3 (25%)	12
Rembach (*M*. aff. *collongensis*)		8 (73%)	3 (27%)	11
Rauscheröd 1b, 1c, 1d (*M*. aff. *collongensis*)	2 (9%)	14 (64%)	6 (27%)	22
Sandelzhausen (*M.* aff. *bavaricus)*		7 (70%)	3 (30%)	10
Sansan (*M.gersii*)		5 (63%)	3 (38%)	8
Châteauredon (*M.lalaï*)	2 (4%)	31 (67%)	13 (28%)	46
La Romieu-Soucaret (*M. bezianensis*)	5 (29%)	11 (65%)	1 (6%)	17
Bézian (*M. bezianensis*)	5 (14%)	28 (76%)	4 (11%)	37
Pellecahus (*M. bezianensis*)		1 (50%)	1 (50%)	2
Valdemoros 8A	6 (15%)	29 (73%)	5 (13%)	40
Moratilla 3	1 (33%)	2 (67%)		3
Moratilla 2		8 (57%)	6 (43%)	14
Fuente Sierra 4	2 (29%)	5 (71%)		7
La Retama	1 (33%)		2 (67%)	3
La Col-D	4 (29%)	5 (36%)	5 (36%)	14

Table 13S. Mesoloph M2

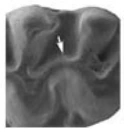
Localities					I	
Niederaichbach (*M.bavaricus*)		2 (100%)			2	2,00
Langenmoosen (*M. bavaricus*)	6 (22%)	18 (67%)	3 (11%)		27	1,89
Forsthart (*M.* aff. *collongensis)*	3 (23%)	8 (62%)	2 (15%)		13	1,92
Rembach (*M*. aff. *collongensis*)	3 (27%)	4 (36%)	4 (36%)		11	2,09
Rauscheröd 1b, 1c, 1d (*M*. aff. *collongensis*)	4 (17%)	10 (43%)	9 (39%)		23	2,22
Sandelzhausen (*M.* aff. *bavaricus)*		3 (30%)	6 (60%)	1 (10%)	10	2,80
Nebelbergweg bei Nunningen (*M. robustus*)		2 (40%)	3 (60%)		5	2,60
Sansan (*M.gersii*)		1 (13%)	7 (88%)		8	2,88
Suèvres (*M.bourgeoisi*)		2 (100%)			2	2,00
Châteauredon (*M.lalaï*)	11 (22%)	32 (64%)	7 (14%)		50	1,92
La Romieu-Soucaret (*M. bezianensis*)	1 (6%)	9 (53%)	7 (41%)		17	2,35
Bézian (*M. bezianensis*)		(100%)				
Pellecahus (*M. bezianensis*)		1 (50%)	1 (50%)		2	2,50
Valdemoros 8A		25 (66%)	13 (34%)		38	2,34
Moratilla 3		4 (80%)	1 (20%)		5	2,20
Moratilla 2	2 (11%)	9 (50%)	7 (39%)		18	2,28
Fuente Sierra 4		3 (43%)	4 (57%)		7	2,57
La Retama		2 (67%)	1 (33%)		3	2,33
La Col-D	1 (7%)	8 (57%)	5 (36%)		14	2,29

Table 14S. Connection Mesolph-Ectoloph M2

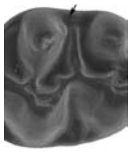
Localities				N
Langenmoosen (*M. bavaricus*)	11 (41%)	15 (56%)	1 (4%)	27
Forsthart (*M.* aff. *collongensis)*	2 (15%)	10 (77%)	1 (8%)	13
Rembach (*M*. aff. *collongensis*)	4 (36%)	7 (64%)		11
Rauscheröd 1b, 1c, 1d (*M*. aff. *collongensis*)	6 (29%)	13 (62%)	2 (10%)	21
Nebelbergweg bei Nunningen (*M. robustus*)	2 (67%)	1 (33%)		3
Sandelzhausen (*M.* aff. *bavaricus)*	3 (30%)	7 (70%)		10
Sansan (*M.gersii*)	4 (50%)	4 (50%)		8
Suèvres (*M.bourgeoisi*)	1 (33%)	2	(86%) (46%)	3
Châteauredon (*M.lalaï*)	20 (45%)	22 (50%)	2 (5%)	44
La Romieu-Soucaret (*M. bezianensis*)	3 (18%)	9 (53%)	5 (29%)	17
Bézian (*M. bezianensis*)	5 (7%)	65	(93%)	70
Pellecahus (*M. bezianensis*)		2 (100%)		2
Valdemoros 8A	7 (21%)	22 (65%)	5 (15%)	34
Moratilla 3		2 (67%)	1 (33%)	3
Moratilla 2	2 (14%)	12 (86%)		14
Fuente Sierra 4		5 (71%)	2 (29%)	7
La Retama	1 (33%)	1 (33%)	1 (33%)	3
La Col-D	1 (7%)	9 (64%)	4 (29%)	14

Table 15S. Metalophule M2

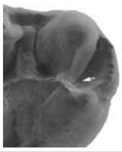
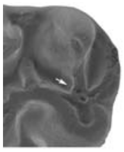
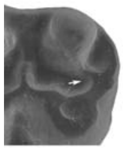
Localities								N
Langenmoosen (*M. bavaricus*)		14 (61%)	1 (4%)		5 (22%)	2 (9%)	1 (4%)	23
Forsthart (*M.* aff. *collongensis*)		9 (90%)		1 (10%)				10
Rembach (*M.* aff. *collongensis*)		7 (70%)		3 (30%)				10
Rauscheröd 1b, 1c, 1d (*M* . aff. *collongensis*)	1 (6%)	11 (61%)		2 (11%)	2 (11%)	1 (6%)	1 (6%)	18
Sandelzhausen (*M.* aff. *bavaricus*)		5 (50%)		2 (20%)	3 (30%)			10
Sansan (*M. gersii*)		5 (100%)						5
Suèvres (*M. bourgeoisi*)				1 (50%)	1 (50%)			2
Châteauredon (*M. lalai*)		37 (77%)		9 (19%)	2 (4%)			48
La Romieu-Soucaret (*M. bezianensis*)		15 (94%)			1 (6%)			16
Bézian (*M. bezianensis*)		51 (73%)		7 (10%)	12 (17%)			70
Pellecahus (*M. bezianensis*)		1 (50%)			1 (50%)			2
Valdemoros 8A		28 (85%)		3 (9%)	2 (6%)			33
Moratilla 3		1 (50%)			1 (50%)			2
Moratilla 2		11 (61%)		3 (17%)	4 (22%)			18
Fuente Sierra 4		5 (83%)			1 (17%)			6
La Retama		3 (100%)						3
La Col-D	1 (8%)	8 (62%)		3 (23%)	1 (8%)			13

Table 16S. Metalophule M3

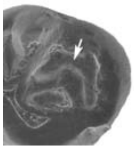
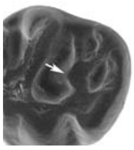
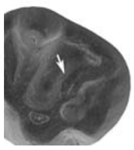
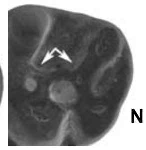
Localities								N
Niederaichbach (*M. bavaricus*)			2 100%					2
Langenmoosen (*M. bavaricus*)	4 (33%)	3 (25%)	2 (17%)	2 (25%)			1 (8%)	12
Rembach (*M.* aff. *collongensis*)	4 (67%)		1 (17%)		1 (17%)			6
Rauscheröd 1b, 1c, 1d (*M* . aff. *collongensis*)	6 (60%)		1 (10%)		3 (30%)			10
Blanquatère 1 (*M. aunayi*)	3 (19%)	2 (13%)	11 (69%)					16
Châteauredon (*M. lalai*)	1 (5%)	2 (10%)	11 (55%)	2 (11%)		1 (5%)	3 (15%)	20
La Romieu-Soucaret (*M. bezianensis*)	2 (67%)		1 (33%)					3
Valdemoros 8A		2 (40%)	2 (40%)		1 (20%)			5
Moratilla 3								
Moratilla 2	1 (9%)	4 (36%)	3 (27%)		3 (27%)			11
Fuente Sierra 4								
La Retama		2 100%						2
La Col-D			1 (20%)	1 (20%)	3 (60%)			5

Table 17S. Anteroconid m1

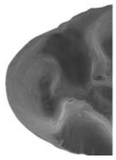
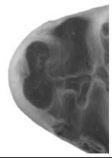
Localities				N
Niederaichbach (*M.bavaricus*)	1 (100%)			1
Langenmoosen (*M. bavaricus*)	15 (47%)	11 (34%)	6 (19%)	32
Forsthart (*M.* aff. *collongensis)*	7 (78%)	2 (22%)		9
Rembach (*M* . aff. *collongensis*)	9 (69%)	4 (31%)		13
Rauscheröd 1b, 1c, 1d (*M* . aff. *collongensis*)	9 (69%)	4 (31%)		13
Sandelzhausen (*M.* aff. *bavaricus)*		2 (22%)	7 (78%)	9
Blanquatère 1 (*M. aunayi*)	89 (68%)	38 (29%)	4 (3%)	131
Blanquatère 1 (*M. "collongensis-gersii"*)	71 (85%)	12 (14%)	1 (1%)	84
Sansan (*M.gersii*)	4 (21%)	12 (63%)	3 (16%)	19
Châteauredon (*M.lalaï*)	42 (98%)	1 (2%)		43
Suèvres (*M.bourgeoisi*)	(100%)			
La Romieu-Soucaret (*M. bezianensis*)	17 (77%)	5 (23%)		22
Bézian (*M. bezianensis*)	62 (85%)	11 (15%)		73
Pellecahus (*M. bezianensis*)	1 (100%)			1
Valdemoros 8A	17 (71%)	5 (21%)	2 (8%)	24
Moratilla 3	2 (100%)			2
Moratilla 2	14 (82%)	2 (12%)	1 (6%)	17
Fuente Sierra 4	11 (92%)	1 (8%)		12
La Retama	5 (63%)	3 (38%)		8
La Col-D	8 (80%)	2 (20%)		10

Table 18S. Labial Spur of the Anterolophulid m1

Localities				N
Niederaichbach (*M.bavaricus*)	2 (100%)			2
Langenmoosen (*M. bavaricus*)	8 (25%)	1 (3%)	23 (72%)	32
Forsthart (*M.* aff. *collongensis)*	6 (60%)		4 (40%)	10
Rembach (*M* . aff. *collongensis*)	6 (50%)	1 (8%)	5 (42%)	12
Rauscheröd 1b, 1c, 1d (*M* . aff. *collongensis*)	11 (73%)		4 (27%)	15
Sandelzhausen (*M.* aff. *bavaricus)*	7 (78%)		2 (22%)	9
Blanquatère 1 (*M. aunayi*)	112 (84%)	3 (2%)	18 (14%)	133
Blanquatère 1 (*M. "collongensis-gersii"*)	63 (76%)	3 (4%)	17 (20%)	83
Sansan (*M.gersii*)	23 (96%)		1 (4%)	24
Châteauredon (*M.lalaï*)	28 (64%)	6 (14%)	10 (23%)	44
La Romieu-Soucaret (*M. bezianensis*)	17 (81%)		4 (19%)	21
Bézian (*M. bezianensis*)	64 (88%)		9 (12%)	73
Pellecahus (*M. bezianensis*)			1 (100%)	1
Valdemoros 8A	15 (52%)	5 (15%)	14 (48%)	34
Moratilla 3	2 (67%)		1 (33%)	3
Moratilla 2	19 (73%)		7 (27%)	26
Fuente Sierra 4	10 (83%)		2 (17%)	12
La Retama	4 (50%)		4 (50%)	8
La Col-D	13 (87%)		2 (13%)	15

Table 19S. Metalophulid m1

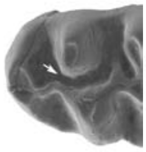
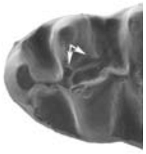
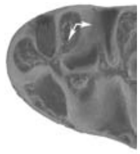
Localities						N
Niederaichbach (*M. bavaricus*)			2 (100%)			2
Langenmoosen (*M. bavaricus*)			33 (100%)			33
Forsthart (*M.* aff. *collongensis*)			11 (100%)			11
Rembach (*M*. aff. *collongensis*)			13 (93%)	1 (7%)		14
Rauscheröd 1b, 1c, 1d (*M* . aff. *collongensis*)			16 (94%)	1 (6%)		17
Sandelzhausen (*M.*aff. *bavaricus*)			9 (100%)			9
Blanquatère 1 (*M. aunayi*)	1 (1%)		101 (91%)	3 (3%)	6 (5%)	111
Blanquatère 1 (*M. "collongensis-gersii"*)		1 (1%)	71 (91%)	4 (5%)	2 (3%)	78
Sansan (*M. gersii*)	1 (3%)		17 (85%)	1 (5%)	1 (5%)	20
Châteauredon (*M .lalai*)			45 (100%)			45
Suèvres (*M.bourgeoisi*)			(100%)			
La Romieu-Soucaret (*M. bezianensis*)	1 (3%)		18 (95%)			19
Bézian (*M. bezianensis*)			73 (100%)			73
Pellecahus (*M. bezianensis*)					1 (100%)	1
Valdemoros 8A			25 (86%)	4 (14%)		29
Moratilla 3			3 (100%)			3
Moratilla 2			14 (100%)			14
Fuente Sierra 4			10 (83%)	2 (17%)		12
La Retama			8 (100%)			8
La Col-D			11 (61%)	3 (17%)	4 (22%)	18

Table 20S. Mesolophid m1

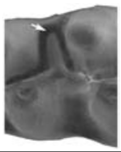
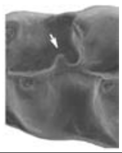
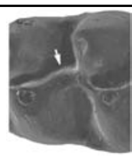
Localities					N
Niederaichbach (*M.bavaricus*)		2 (100%)			2
Langenmoosen (*M. bavaricus*)	2 (6%)	12 (36%)	18 (55%)	1 (3%)	33
Forsthart (*M.* aff. *collongensis)*		5 (38%)	8 (62%)		13
Rembach (*M*. aff. *collongensis*)		2 (14%)	12 (86%)		14
Rauscheröd 1b, 1c, 1d (*M*. aff. *collongensis*)		4 (21%)	13 (68%)	2 (11%)	19
Nebelbergweg bei Nunningen (*M. robustus*)				6 (100%)	6
Sandelzhausen (*M.* aff. *bavaricus)*		1 (11%)	6 (67%)	2 (22%)	9
Blanquatère 1 (*M. aunayi*)		15 (12%)	90 (72%)	20 (16%)	125
Blanquatère 1 (*M. "collongensis-gersii"*)		10 (12%)	64 (79%)	7 (9%)	81
Sansan (*M.gersii*)		2 (10%)	16 (76%)	3 (14%)	21
Châteauredon (*M.lalaï*)		16 (36%)	29 (64%)		45
La Romieu-Soucaret (*M. bezianensis*)		5 (24%)	15 (71%)	1 (5%)	21
Bézian (*M. bezianensis*)		52 (72%)	20 (28%)		72
Pellecahus (*M. bezianensis*)			1 (100%)		1
Valdemoros 8A		6 (16%)	31 (84%)		37
Moratilla 3			3 (100%)		3
Moratilla 2		4 (17%)	20 (83%)		24
Fuente Sierra 4		6 (50%)	6 (50%)		12
La Retama			8 (100%)		8
La Col-D	1 (5%)	6 (32%)	12 (63%)		19

Table 21S. Ectomesolophid m1

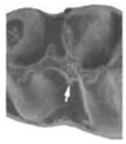
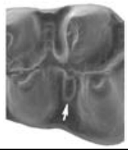
Localities				N
Niederaichbach (*M.bavaricus*)	2 (100%)			2
Langenmoosen (*M. bavaricus*)	34 (97%)	1 (3%)		35
Forsthart (*M.* aff. *collongensis)*	12 (92%)		1 (8%)	13
Rembach (*M*. aff. *collongensis*)	13 (93%)		1 (7%)	14
Rauscheröd 1b, 1c, 1d (*M*. aff. *collongensis*)	14 (82%)	1 (6%)	2 (12%)	17
Sandelzhausen (*M.* aff. *bavaricus)*	8 (89%)		1 (11%)	9
Blanquatère 1 (*M. aunayi*)	157 (100%)			157
Blanquatère 1 (*M. "collongensis-gersii"*)	86 (97%)	2 (2%)	1 (1%)	89
Sansan (*M.gersii*)	24 (100%)			24
Châteauredon (*M.lalaï*)	48 (100%)			48
La Romieu-Soucaret (*M. bezianensis*)	18 (90%)		2 (10%)	20
Pellecahus (*M. bezianensis*)	1 (100%)			1
Valdemoros 8A	38 (100%)			38
Moratilla 3	5 (100%)			5
Moratilla 2	26 (100%)			26
Fuente Sierra 4	13 (100%)			13
La Retama	8 (100%)			8
La Col-D	15 (75%)	4 (20%)	1 (5%)	20

Table 22S. Lingual Anterolophid m2

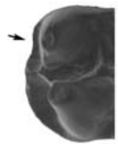
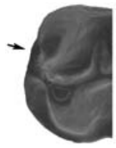
Localities				N
Niederaichbach (*M.bavaricus*)		4 (100%)		4
Langenmoosen (*M. bavaricus*)	5 (19%)	22 (81%)		27
Forsthart (*M.* aff. *collongensis)*	2 (22%)	7 (78%)		9
Rembach (*M*. aff. *collongensis*)	4 (29%)	10 (71%)		14
Rauscheröd 1b, 1c, 1d (*M*. aff. *collongensis*)	5 (22%)	17 (74%)	1 (4%)	23
Sandelzhausen (*M.* aff. *bavaricus)*		5 (100%)		5
Blanquatère 1 (*M. tautavelensis*)	16 (31%)	33 (63%)	3 (6%)	52
Sansan (*M.gersii*)	2 (9%)	20 (87%)	1 (4%)	23
Châteauredon (*M.lalaï*)	9 (15%)	47 (80%)	3 (5%)	59
La Romieu-Soucaret (*M. bezianensis*)	1 (25%)	2 (50%)	1 (25%)	4
Valdemoros 8A	1 (4%)	23 (82%)	4 (14%)	28
Moratilla 3		5 (100%)		5
Moratilla 2		6 (86%)	1 (14%)	7
Fuente Sierra 4		10 (91%)	1 (9%)	11
La Retama		5 (100%)		5
La Col-D		10 (100%)		10

Table 23S. Mesolophid m2

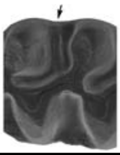
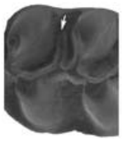
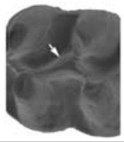
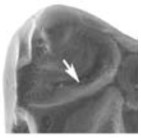
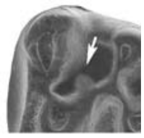
Localities					N
Niederaichbach (*M.bavaricus*)			4 (100%)		4
Langenmoosen (*M. bavaricus*)		8 (24%)	26 (76%)		34
Forsthart (*M.* aff. *collongensis)*		3 (27%)	8 (73%)		11
Rembach (*M*. aff. *collongensis*)		2 (13%)	13 (87%)		15
Rauscheröd 1b, 1c, 1d (*M*. aff. *collongensis*)		5 (17%)	23 (79%)	1 (3%)	29
Nebelbergweg bei Nunningen (*M.robustus*)				4 (100%)	4
Sandelzhausen (*M.* aff. *bavaricus)*		1 (20%)	2 (40%)	2 (40%)	5
Blanquatère 1 (*M. tautavelensis*)	1 (1%)	6 (8%)	47 (66%)	17 (24%)	71
Sansan (*M.gersii*)		8 (27%)	21 (70%)	1 (3%)	30
Châteauredon (*M.lalaï*)		13 (21%)	43 (69%)	6 (10%)	62
La Romieu-Soucaret (*M. bezianensis*)	1 (25%)	1 (25%)	1 (25%)	1 (25%)	4
Bézian (*M. bezianensis*)		6 (20%)	23 (77%)	1 (3%)	30
Valdemoros 8A		2 (5%)	36 (95%)		38
Moratilla 3		2 (29%)	5 (71%)		7
Moratilla 2			10 (100%)		10
Fuente Sierra 4		1 (8%)	11 (92%)		12
La Retama			4 (100%)		4
La Col-D			11 (100%)		11

Table 24S. Mesolophid m3

Localities				N
Niederaichbach (*M.bavaricus*)	1 (100%)			1
Langenmoosen (*M. bavaricus*)	10 (83%)	1 (8%)	1 (8%)	12
Rembach (*M*. aff. *collongensis*)	7 (70%)		3 (30%)	10
Rauscheröd 1b, 1c, 1d (*M*. aff. *collongensis*)	14 (93%)		1 (7%)	15
Sandelzhausen (*M.* aff. *bavaricus)*	1 (100%)			1
Sansan (*M.gersii*)	2 (100%)			2
Châteauredon (*M.lalaï*)	30 (83%)	3 (8%)	3 (8%)	36
La Romieu-Soucaret (*M. bezianensis*)	2 (100%)			2
Bézian (*M. bezianensis*)	63 (95%)		3 (5%)	66
Pellecahus (*M. bezianensis*)	2 (100%)			2
Valdemoros 8A	14 (93%)		1 (7%)	15
Moratilla 3				
Moratilla 2	17 (89%)		2 (11%)	19
Fuente Sierra 4	3 (100%)			3
La Retama	2 (100%)			2
La Col-D	3 (100%)			3

4. *Megacricetodon primitivus*

4.1. INTRODUCTION

The genus *Megacricetodon* has been profusely used to propose continental biostratigaphic and biocronologic scales for the early and middle Miocene of Europe, based on its broad geographic distribution as well as its quick changes in size and morphology. Since its definition by Fahlbusch (1964), several *Megacricetodon* lineages have been proposed showing evolutionary patterns that involve strong changes in size and morphology (Aguilar, 1995; Daams & Freudenthal, 1988a; Abdul Aziz et al., 2010). According to most of the authors the genus *Megacricetodon* shows a strong provincialism, implying quite independent evolution within the different European areas. Examples of the different lineages proposed for the early and middle Miocene are the German *M. bavaricus- M. lappi* lineage (Heissig 1990, 1997; Abdul-Aziz et al 2010), The French *M. collongensis- M. rousillonensis* lineage (Aguilar, 1995) and the Spanish *M. primitivus- M. ibericus* lineage (Daams & Freudenthal, 1988a), Nevertheless, recent studies have shown that the exchanges between areas were more frequent than previously thought (Oliver & Pelaez-Campomanes, 2013).

This work will focus on the early representatives of the genus *Megacricetodon* from the Calatayud-Montalban basin included by Daams & Freudenthal (1988a) in the *M. primitivus- M. ibericus* lineage. According to these authors, and based on a small number of localities, the material from the lower and middle Aragonian belong to two successive species: *M. primitivus* and *M. collongensis*. The species *Megacricetodon primitivus* was defined by Freudenthal (1963) on the basis of material from the locality of Valtorres, in the Calatayud-Montalbán Basin (NE of the Iberian Peninsula). Freudenthal (1963) and Daams & Freudenthal (1988a) proposed that this species was part of the lineage *M. primitivus- M. ibericus* that evolved into *M. collongensis*. However, later work, (Daams et al., 1998; Daams et al., 1999a), informally proposed that *M. primitivus* and *M. collongensis* were synonymous.

Nowadays, with more than 100 fossil sites, the Calatayud Montalbán Basin is one of the basins with the better Miocene small mammal fossil record of the world in number of localities as well as in abundance of Miocene mammal fossils (Daams et al., 1999a, van der Meulen et al., 2012). Oliver Pérez et al. (2008) studied the earliest representative of *Megacricetodon* of the basin from the locality of Artesilla (lower Aragonian, local zone Ca), and rejected the synonymy between *M. primitivus* and *M. collongensis*, provisionally attributing the material from this locality to *M. primitivus*. Other works on *Megacricetodon* from the Calatayud-Montalbán Basin (Oliver et al., 2009a,b) further confirm that the two species are different. The detailed study of the *Megacricetodon* from the Aragonian allowed van der Meulen et al. (2012) to update the biostratigraphy of the lower and middle

Aragonian, formally redefining the Spanish local zones, and determining exactly the range of *M. primitivus*.

Objective of the chapter:

-Show the evolutionary patterns of *Megacricetodon primitivus* in Spain since its first occurrence in the Calatayud-Montalbán Basin in the lower Aragonian (local zone Ca) to its last occurrence in middle Aragonian (local zone Db). For this purpose we have checked and described the type material from Valtorres, studied other localities from the Calatayud-Montalbán Basin not previously described, and have compared it with other assemblages of *M. primitivus* from European basins both in and outside Spain.

4.2. MATERIAL

We have studied the available material from the type locality of Valtorres: the type material published by Freudenthal in 1963, the extra material in the collections of the Faculty of Earth Sciences in the University of Utrecht and the collection from Valtorres belonging to the Museo Nacional de Ciencias Naturales-CSIC, Madrid.

We have also studied the material of *Megacricetodon primitivus* from the following localities in the Caltayud-Montalbán Basin: Artesilla, San Roque 3, Olmo Redondo 4A, Vargas 4A, Vargas 4B, Vargas 4BB, Vargas 1A, Vargas 3, Olmo Redondo 5, Olmo Redondo 8, Vargas 2A, La Col-A, Vargas 2B, Olmo Redondo 9, Fuente Sierra 2, Fuente Sierra 3, La Col B, La Col C, La Col D, Fuente Sierra 4 and Valdemoros 8A in the Aragonian type area (Zaragoza); Moratilla 2 and Moratilla 3 in the Calamocha area (Teruel); and from the locality of La Retama in the Loranca Basin.

In addition, other collections of *Megacricetodon* from other Spanish and European basins have been included and studied in detail, and the assignment to this species is discussed.

4.3. RESULTS AND DISCUSSION

Megacricetodon primitivus (Freudenthal, 1963) is the first representative of the genus in Spain. This first occurrence is combined with the first and last occurrences of several taxa such as *Ligerimys florancei*, *Praearmantomys crusafonti*, *Armantomys jasperi* and *Simplomys robustus* (van der Meulen et al., 2012), representing an important period of high turnover on the rodent community (Daams et al., 1999b; van der Meulen et al., 2005). Moreover, in classical publications *M. primitivus* was supposed to be the earliest representative of the genus, from which other species of *Megacricetodon* evolved. Prior to

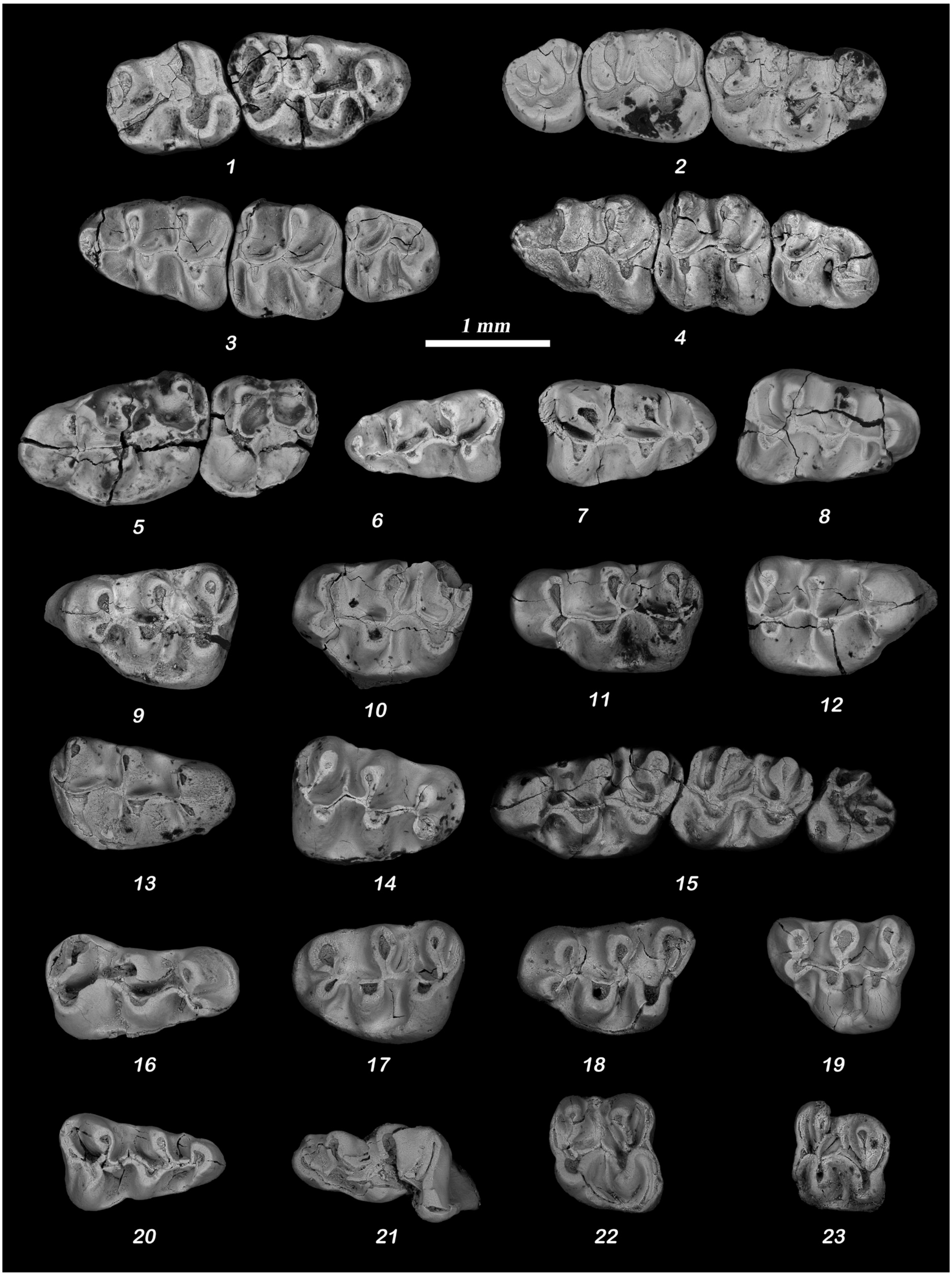


Figure 4.1. *Megacricetodon primitivus* from Valtorres with different types of deformations. Type material: 1, VLT-56-25 M1-M2 right; 2, VLT-56-28 M1-M3 right; 3, VLT-56-132 m1-m3 left; 4, VLT-56-140 m1-m3 left; 5, VLT-56-146 M1-M2 left; 6, VLT-56-159 m1 left; 7, VLT-56-160 m1 right; 8, VLT-56-170 m1 right; 9, VLT-56-192 M1 left; 10, VLT-56-193 M1 left; 11, VLT-56-194 M1 left; 12, VLT-56-198 M1 right; 13, VLT-56-207 M1 right; 14, VLT-56-209 M1 right. Extra material found in the collections of the Utrecht University: 15, VLT-1.2 M1-M3 left. Collection of Valtorres belonging to the Museo Nacional de Ciencias Naturales-CSIC: 16, VLT-MNCN-0.1 M1 right; 17, VLT-MNCN-1.0 M1 left; 18, VLT-MNCN-1.1 M1 left; 19, VLT-MNCN-1.2 M1 left; 20, VLT-MNCN-1.8 m1 right; 21, VLT-MNCN-2.2 m1 left; 22, VLT-MNCN-3.2 M2 right; 23, VLT-MNCN-4.0 M2 left. The photographs were made with a Scanning Electron Microscope using a backscattered electron detector (BSED). All of the teeth are at the same magnification. Scale bar equals 1 mm.

discuss the evolutionary patterns of this species, a detailed description and discussion on the material from the type locality is needed. As will be shown below, the type material shows strong taphonomical deformations that affect the metrical variability published on the original description.

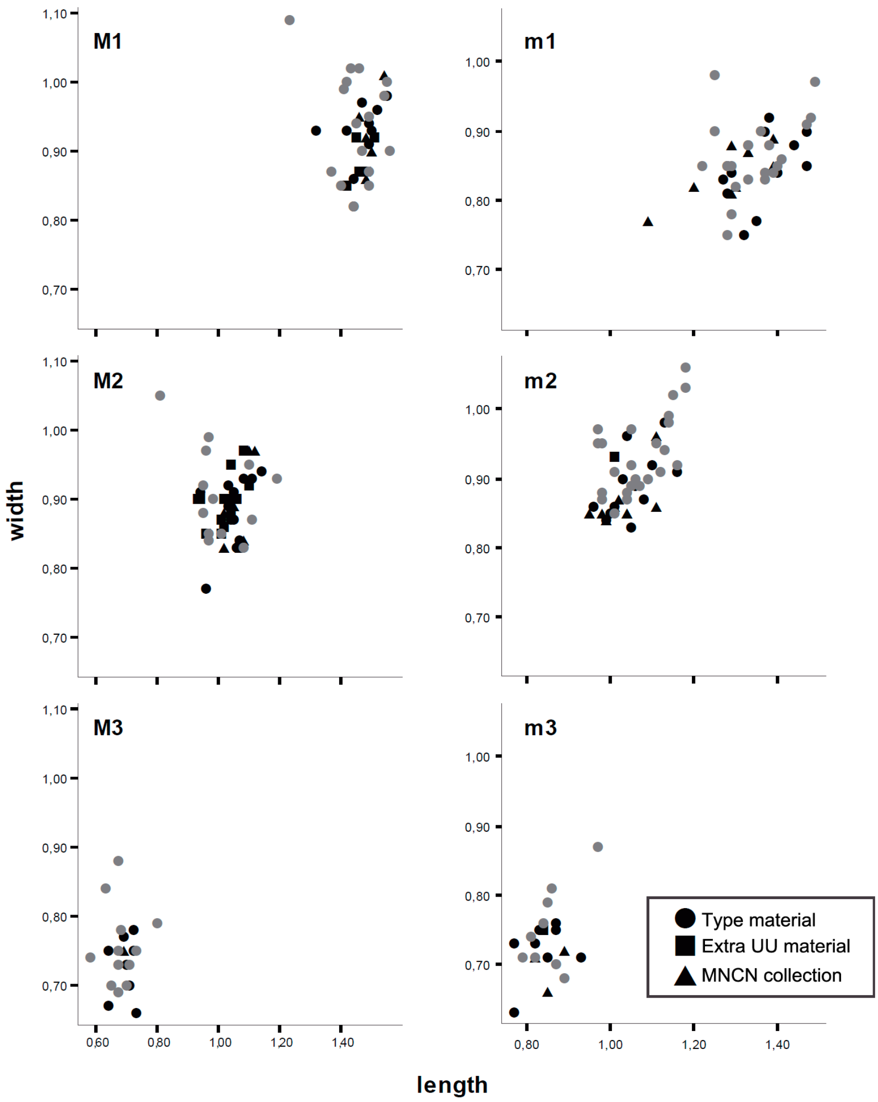


Figure 4.2. Scatterplot of length versus width of the jugal teeth of Valtorres. Circle: Valtorres type material published by Freudenthal (1963); Square: Extra material found in the collections of the Utrecht University; Triangle: Collection of Valtorres belonging to the Museo Nacional de Ciencias Naturales-CSIC; in black: Are represented the measures after having removed the broken, deformed and corroded teeth; and in grey: Are represented the measures taken by Freudenthal, 1963.

Remarks on Megacricetodon primitivus *from Valtorres*

The locality of Valtorres where *M. primitivus* has been described is a peculiar site. The fossils found there show strong deformation and fractures. Figure 4.1 show different types of deformation: such as occlusal deformation (Figure 1: 5, 8-12), bucco-lingual compression (Figure 4.1: 16, 20), antero-posterior compression (Figure 4.1: 19, 23) or torsion (Figure 4.1: 21). These processes have strongly affected the size of a significant number of specimens, producing an overestimation or underestimation of length and width. Figure 4.2 show length/width scatter plots of the different dental elements from Valtorres, including the type material published by Freudenthal (1963), the extra material found in the collections of the Utrecht University, and the collection from Valtorres belonging to the Museo Nacional de Ciencias Naturales-CSIC. These scatter plots show the distribution of the strongly deformed material (in grey) in relation with the remaining specimens used for the calculation of the descriptive statistics. Finally, Table 4.1 and 4.2 show the measures of *M. primitivus* after having removed the broken, deformed and corroded teeth.

4.4. SYSTEMATIC PALAEONTOLOGY

Order RODENTIA Bowdich, 1821

Family MURIDAE Illiger, 1811

Subfamily CRICETODONTINAE Schaub, 1925

Genre *Megacricetodon* Fahlbusch, 1964

Megacricetodon primitivus (Freudenthal 1963)

(Figure 4.3: 1 to 37)

Original diagnosis (Freudenthal, 1963, English translation from Daams & Freudenthal, 1988a): Three out of 36 m1 have an ectomesolophid. In five out of 15 m3 a weak mesolophid or a remnant of the posterior metalophulid is present. In other respects this species agrees with *M. minor*.

Emended diagnosis: Small-sized species of *Megacricetodon*. Lower first molars with rounded anteroconid, generally simple; short anterolophulid, ectomesolophid generally absent. The m3 mesoloph present in low frequency. Upper first molars with an anterocone always double, normally with a small platform in front of the furrow; a strong lingual mesocingulum that connects the hypocone to the anterocone in more than 20% of the specimens; mesoloph normally short to medium.

Differential diagnosis: *Megacricetodon primitivus* differs from the large-sized group of *Megacricetodon* defined by Peláez-Campomanes & Daams (2002) by its significantly smaller dimension.

Megacricetodon primitivus differs from *M. aguilari* Lindsay, 1988, *M. andrewsi* Peláez-Campomanes & Daams, 2002, *M. crisiensis* Radulescu & Samson, 1988, *M. beijiangensis* Maridet et al., 2011, *M. sivalensis* Lindsay, 1988, *M. similis* (Fahlbusch, 1964), *M. yei* Bi et al., 2008, by its smaller dimension.

Megacricetodon collongensis, (Mein, 1958) is similar in size to *M. primitivus*, but, it differs from it by a higher percentage of double anteroconid, the longer mesolophs(ids), the anterocone of the M1 symmetrically divided, a higher percentage of double protolophule and metalophule in the M1 and M2.

Megacricetodon drebruijni, Freudenthal, 1968, differs from *M. primitivus* by the subdivided anteroconid in the m1 and the shorter mesolophids.

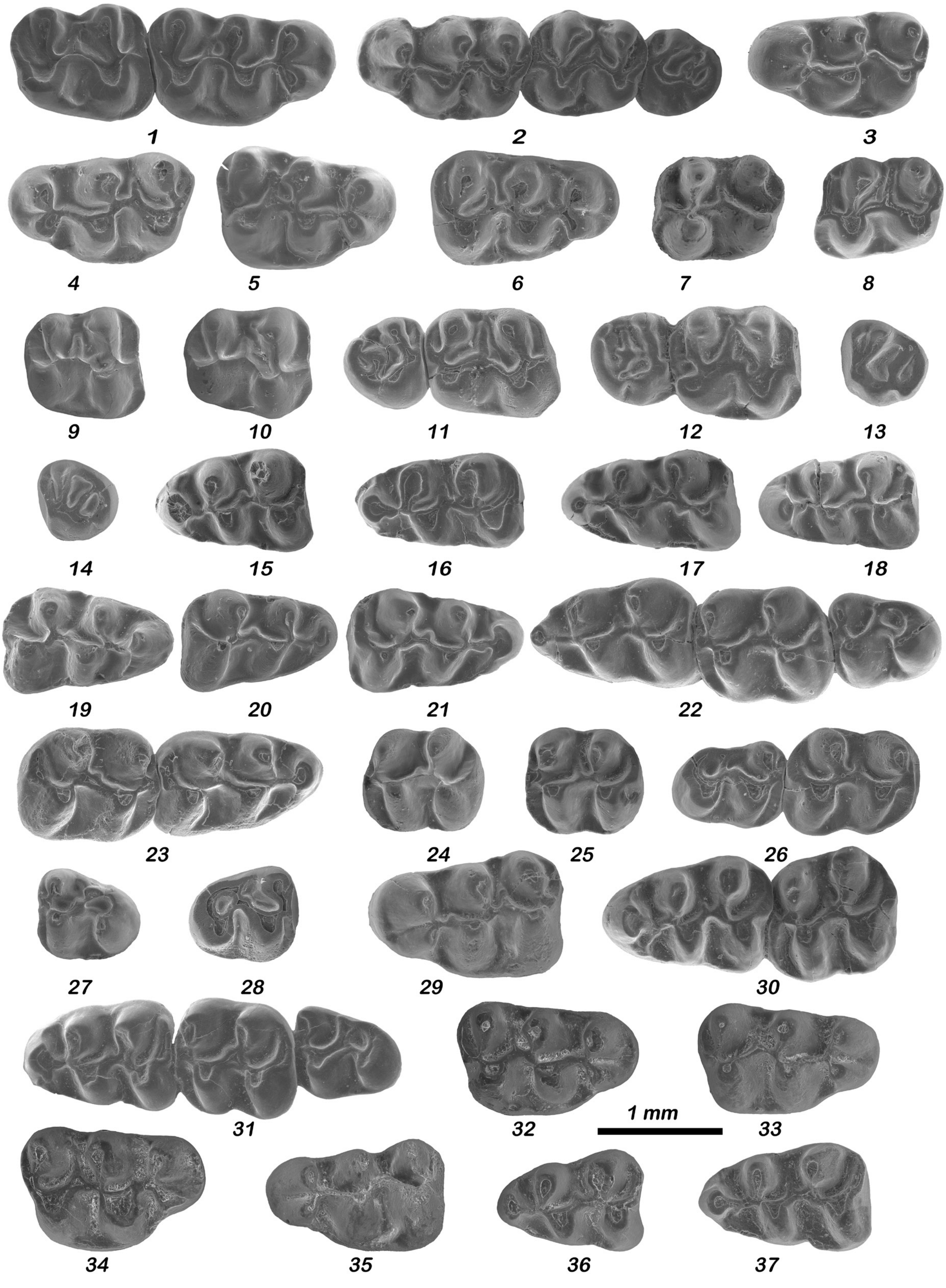


Figure 4.3. *Megacricetodon primitivus* from the type locality of Valtorres. Type material: 1, VLT-56-20 M1-M2 right; 2, VLT-56-21 M1-M3 left; 3, VLT-56-191 M1left; 4, VLT-56-195 M1 left; 5, VLT-56-203 M1 right; 6, VLT-56-206 M1 right; 7, VLT-56-211 M2 left; 8, VLT-56-216 M2 left; 9, VLT-56-225 M2 right; 10, VLT-56-226 M2 right; 11, VLT-56-26 M2-M3 right; 12, VLT-56-29 M2-M3 right; 13- VLT-56-230 M3 left; 14, VLT-56-232 M3 left; 15, VLT-56-131 m1 left; 16, VLT-56-151 m1 left; 17, VLT-56-156 m1 left; 18, VLT-56-157 m1 left; 19, VLT-56-167 m1 right; 20, VLT-56-168 m1 right; 21, VLT-56-169 m1 right; 22, VLT-56-138 m1-m3 left; 23, VLT-56-141 m1-m2 right; 24, VLT-56-171 m2 left; 25, VLT-56-179 m2 left; 26, VLT-56-144 m2-m3 right; 27, VLT-56-42 m3 left; 28, VLT-56-47 m3 right. Extra material founding in the collections of the Utrecht University: 29, VLT-1.3 M1 left; 30, VLT-1.6 m1-m2 left; 31, VLT-1.7 m1-m3 left. Collection of Valtorres belonging to the Museo Nacional de Ciencias Naturales-CSIC: 32, VLT-MNCN-0.3 M1 right; 33, VLT-MNCN-0.4 M1 right; 34, VLT-MNCN-0.5 M1 right; 35, VLT-MNCN-0.8 M1 left; 36, VLT-MNCN-2.3 m1 left; 37, VLT-MNCN-2.6 m1 left. All of the teeth are at the same magnification. Scale bar equals 1 mm.

Megacricetodon primitivus differs from *M. freudenthali* García Moreno (in Álvarez-Sierra & García-Moreno, 1986), *M. lopezae* García-Moreno (in Álvarez-Sierra & García-Moreno, 1986), *M. minor* (Lartet, 1851), *M. minutus* Daxner, 1967, and *M. rafaeli* Daams & Freudenthal, 1988a, by the morphology of the anterocone (anterocone deeply split in *M. primitivus* and simple or slightly split in the others).

Megacricetodon daamsi Lindsay, 1988, differs from *M. primitivus*, by the robust M1 with slightly split anterocone and the shorter mesolophid in the m1.

Megacricetodon pussillus Qiu, 1996, is similarin size to *M. primitivus*, but differs from it by the shorter mesolophid in the m1, the lingual anterolophid always long in the m2, and a cuspidate entoconid in the m3.

Megacricetodon sinensis Qiu et al., 1981, differ from *M. primitivus* by the longer mesoloph in the M2, more complicated and molariform the morphology of the M3, the better-developed labial anterolophid of the m1 and the lower percentage of mesolophid in the m1 and m2.

Megacricetodon tautavelensis Lazzari & Aguilar, 2007, differs from *M. primitivus*, by its smaller size, the higher percentage of slightly split anterocone, and the shorter mesolphs (ids) in the upper and lower first molars and the higher percentage of "crescent"-shaped anteroconid.

Megacrietodon yenicekentensis Erten et al., 2014, differs from *M. primitivus* by having a forked anterolophule in the M1 and long mesolophs in the upper molars.

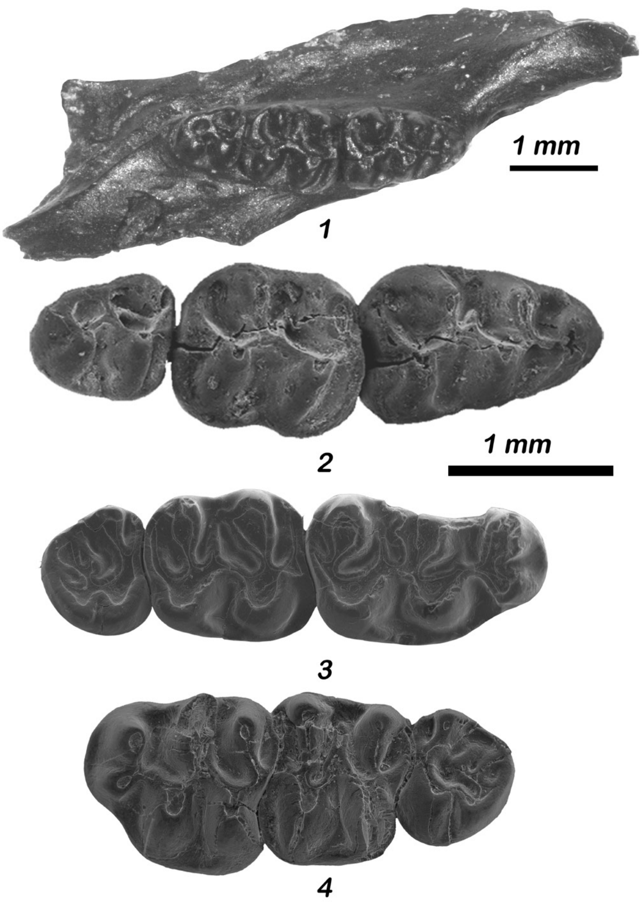


Figure 4.4. *Megacricetodon primitivus* from Valtorres figured by Freudenthal (1963). 1, Right mandible with m1-m3, 56-142, Holotype (light microscope photographs taken with a Leica Mz 95 with a Leica DFC420 digital camera); 2, Right m1-m3 from the Holotype 56-142 (photography donated by the Institut Català de Paleontologia); 3, Right maxilla with M1-M3, 56-28, Paratype; 4, Left maxilla with M1-M3, 56-145, Paratype. Scale bar equals 1 mm.

Holotype: Mandible m1-m3 56-142 (Figure 4.4 A-B). Figured in Freudenthal (1963), Plate 1, fig. 3.

Type locality: Valtorres, Calatayud-Montalbán Basin, Spain (local zone Da, middle Aragonian, middle Miocene).

Stratigraphical distribution: Local zone Ca (lower Aragonian, lower Miocene) to local zone Db (middle Aragonian, middle Miocene).

Geographical distribution: Spain, France, Portugal.

Measurements: Table 4.1 and 4.2 show the descriptive statistics of the upper and lower molars of *Megacricetodon primitivus* from the different localities studied in the Calatayud-Montalbán Basin. We especially emphasize in the site of Valtorres, showing the measures of the Valtorres type material, the extra material of Valtorres from the University of Utrecht, the collection of Valtorres from the MNCN and the global measures of Valtorres (the three collections all together).

4.5. DESCRIPTION OF THE TYPE MATERIAL

M1: The anterocone is deeply split in most specimens (42/45), of which 21 have a small platform in front of the furrow and three a small cingulum ridge in front of it. In the remaining three, the anterocone is slightly subdivided with a small platform in front of the furrow. The labial cone of the anterocone is larger than the lingual one in 36 specimens, while the two cones are equal in size in nine specimens. The anterolophule is connected to the lingual cone of the anterocone in 30 specimens or between the two lobes of the anterocone in 19. The labial spur of the anterolophule is present in 10 out of 53, incipient in two and absent in 41. The protolophule is posterior (35/44), posterior almost double (7/44) or double (2/44). The ectoloph is strong in six specimens, short in 27, and absent in 20. A lingual mesocingulum that connects the protocone to the hypocone, is present in 20 specimens (20/54). The mesoloph is long in one out of 50, medium in 20, short in 25 and absent in four. In one out of 50, the ectoloph is connected with the mesoloph, in 26 there is no connection between the ectoloph and the mesoloph, in 18 there is a mesoloph but the ectoloph is absent and in the remaining five there is neither a mesoloph nor an ectoloph. The metalophule is connected to the posteroloph just behind the hypocone in six, is posterior and the metalophule points backwards in 38, and is posterior and the metalophule points backwards more obliquely delimiting a small posterosinus in one.

	LZ	Locality	T. N.	Length N.	Length min	Length mean	Length max	Length σ	Width N.	Width min	Width mean	Width max	Width σ
M1	Dd	VA1A	28	16	1,36	1,47	1,61	0,060	18	0,88	0,95	1,03	0,090
	Dc	VA11	1	1		1,39			1		0,89		
		VA8A	14	11	1,32	1,38	1,49	0,050	14	0,80	0,87	0,95	0,050
		MOR3	3	3	1,35	1,40	1,45		2	0,88		0,92	
	Db	MOR2	7	4	1,23	1,38	1,43	0,100	4	0,84	0,88	0,91	0,030
		FTE4	8	7	1,34	1,40	1,45	0,050	6	0,86	0,91	0,97	0,040
		COLD	73	40	1,28	1,43	1,51	0,050	65	0,80	0,90	0,98	0,040
		COLC	85	49	1,32	1,43	1,55	0,050	52	0,84	0,91	1,01	0,040
		COLB	12	7	1,34	1,40	1,51	0,059	7	0,82	0,88	0,98	0,055
		VLT(a)	58	25	1,32	1,47	1,56	0,060	28	0,81	0,91	1,01	0,050
		VLT(b)	27	19	1,32	1,47	1,56	0,060	22	0,81	0,91	1,01	0,050
		VLT(c)	16	5	1,46	1,49	1,54	0,030	12	0,81	0,91	1,01	0,050
	Da	VLT(d)	15	6	1,35	1,45	1,51	0,060	6	0,85	0,89	0,93	0,030
		FTE3	9	5	1,40	1,42	1,46	0,025	8	0,82	0,93	1,00	0,054
		FTE2	7	3	1,41	1,45	1,48		3	0,93	0,96	1,00	
		OR9	36	24	1,32	1,40	1,50	0,050	30	0,81	0,88	0,96	0,040
		VR2B	11	9	1,32	1,46	1,55	0,070	9	0,85	0,94	1,03	0,060
		COLA	8	4	1,36	1,41	1,45		5	0,83	0,88	0,92	0,036
		VR2A	8	3	1,35	1,42	1,48		4	0,87	0,91	0,96	
		OR8	33	25	1,29	1,40	1,54		31	0,81	0,89	1,00	0,049
		OR5	16	12	1,37	1,46	1,52	0,043	14	0,83	0,91	1,00	0,049
	Cb	VR3	24	12	1,38	1,47	1,56	0,050	18	0,86	0,93	1,00	0,040
		VR1A	73	34	1,23	1,43	1,59	0,060	49	0,80	0,92	1,05	0,040
		VR4BB	33	22	1,35	1,45	1,51	0,050	30	0,85	0,92	0,98	0,040
		VR4B	5	5	1,34	1,44	1,51	0,070	5	0,81	0,90	0,98	0,060
		VR4A	44	28	1,36	1,46	1,55	0,050	34	0,86	0,93	1,01	0,040
		OR4A	13	9	1,46	1,53	1,59	0,040	9	0,94	0,98	1,02	0,030
	Ca	SR3	5	3	1,52	1,54	1,57		3	0,96	0,97	1,00	
		ART	135	91	1,38	1,46	1,58	0,041	109	0,86	0,94	1,01	0,031
M2	Dd	VA1A	17	7	1,05	1,10	1,19	0,050	8	0,89	0,95	1,02	0,080
		VA8A	7	6	0,91	0,98	1,03	0,050	6	0,75	0,84	0,88	0,050
	Db	MOR2	3	1		0,94			1		0,86		
		FTE4	12	12	0,92	0,99	1,04	0,04	11	0,82	0,88	0,95	0,05
		COLD	72	64	0,91	1,00	1,11	0,050	63	0,78	0,88	0,96	0,040
		COLC	58	48	0,94	1,02	1,15	0,045	46	0,81	0,89	0,97	0,036
		COLB	7	6	0,97	1,01	1,06	0,035	5	0,79	0,86	0,95	0,065
		VLT(a)	53	35	0,93	1,04	1,14	0,050	36	0,77	0,89	0,97	0,040
		VLT(b)	28	20	0,94	1,05	1,14	0,050	21	0,77	0,89	0,97	0,050
		VLT(c)	7	6	1,02	1,07	1,12	0,040	6	0,83	0,90	0,97	0,060
	Da	VLT(d)	18	15	0,93	1,03	1,10	0,050	15	0,83	0,89	0,97	0,040
		FTE3	11	7	0,99	1,07	1,15	0,057	8	0,84	0,90	0,95	0,036
		FTE2	11	9	0,97	1,03	1,09	0,042	9	0,83	0,89	0,93	0,034
		OR9	22	21	0,93	0,99	1,12	0,050	22	0,77	0,86	0,95	0,050
		VR2B	10	9	0,97	1,06	1,11	0,040	7	0,81	0,91	0,97	0,060
		COLA	11	9	0,97	1,04	1,07	0,031	10	0,82	0,88	0,92	0,029
		VR2A	16	14	0,93	1,00	1,04	0,030	11	0,80	0,85	0,89	0,030
		OR8	36	33	0,87	0,98	1,11	0,063	34	0,80	0,87	0,95	0,045
		OR5	15	13	0,94	1,01	1,07	0,038	15	0,77	0,88	0,98	0,054
	Cb	VR3	23	20	0,97	1,05	1,13	0,050	19	0,83	0,89	0,94	0,030
		VR1A	74	55	0,93	1,04	1,14	0,050	54	0,83	0,89	0,96	0,030
		VR4BB	35	28	0,99	1,05	1,14	0,040	28	0,84	0,91	0,99	0,040
		VR4B	7	5	1,03	1,07	1,11	0,040	6	0,88	0,90	0,93	0,020
		VR4A	38	28	0,97	1,04	1,13	0,040	31	0,84	0,89	0,94	0,030
		OR4A	14	10	0,97	1,02	1,13	0,050	10	0,92	0,96	1,00	0,030
	Ca	SR3	3	2	1,06		1,10		2	0,99		1,00	
		ART	118	95	0,96	1,05	1,14	0,039	89	0,83	0,91	0,99	0,035
M3	Dd	VA1A	8	4	0,67	0,73	0,78		5	0,72	0,78	0,82	0,040
		COLC	3	2	0,72		0,75		3	0,73	0,75	0,76	
	Da	VLT(a)	22	9	0,64	0,69	0,73	0,030	15	0,66	0,72	0,78	0,040
		VLT(b)	20	9	0,64	0,69	0,73	0,030	15	0,66	0,72	0,78	0,040
		VLT(c)	2	1		0,69			1		0,75		
		OR8	3	3	0,70	0,75	0,78		3	0,75	0,78	0,81	
	Cb	OR5	4	4	0,65	0,69	0,73		4	0,70	0,75	0,80	
		VR1A	4	4	0,68	0,71	0,74		4	0,71	0,74	0,78	
		OR4A	2	1		0,77			2	0,77		0,79	
	Ca	SR3	3	3	0,75	0,78	0,80		3	0,78	0,81	0,85	
		ART	16	14	0,66	0,72	0,80	0,045	15	0,71	0,75	0,79	0,029

Table 4.1. Descriptive statistics of the upper molars of *Megacricetodon primitivus*. Abbreviations: LZ, Local zone; T.N., total number of teeth; N., number of teeth measured; min, minimum; max, maximum; δ, standard deviation. VLT (a), global measures of Valtorres (the three collections: type material + extra UU material + MNCN); VLT (b), Valtorres type material; VLT (c), Valtorres extra UU material; VLT (d), Valtorres MNCN. The measures of VR1A, OR5, OR8 and OR9 are from Daams and Freudenthal (1988a).

	LZ	Locality	T. N.	Length N.	Length min	Length mean	Length max	Length σ	Width N.	Width min	Width mean	Width max	Width σ
m1	**Dd**	VA1A	27	18	1,26	1,33	1,46	0,050	18	0,77	0,85	0,91	0,030
	Dc	MUN3A	2	1		1,32			1		0,82		
		VA8A	4	3	1,19	1,23	1,25		3	0,78	0,80	0,81	
	Db	FTE4	8	6	1,19	1,28	1,36	0,060	7	0,75	0,80	0,84	0,030
		COLD	47	30	1,17	1,28	1,38	0,050	40	0,74	0,81	0,87	0,030
		COLC	69	51	1,18	1,28	1,40	0,051	55	0,75	0,82	0,90	0,036
		COLB	3	1		1,30			2	0,80		0,83	
		VLT(a)	57	21	1,09	1,33	1,47	0,090	33	0,75	0,85	0,96	0,050
		VLT(b)	34	13	1,27	1,35	1,47	0,070	22	0,75	0,86	0,96	0,050
		VLT(c)	8						5	0,84	0,91	0,96	0,050
	Da	VLT(d)	15	8	1,09	1,29	1,39	0,100	11	0,76	0,83	0,89	0,040
		FTE3	6	3	1,22	1,28	1,31		5	0,78	0,83	0,86	0,030
		FTE2	14	11	1,20	1,30	1,38	0,057	12	0,79	0,85	0,90	0,038
		OR9	18	10	1,14	1,23	1,32	0,070	16	0,74	0,81	0,88	0,040
		VR2B	12	4	1,29	1,33	1,36		4	0,84	0,86	0,90	
		COLA	13	6	1,24	1,32	1,36	0,049	9	0,78	0,84	0,88	0,030
		VR2A	7	3	1,20	1,22	1,23		6	0,74	0,80	0,84	0,030
		OR8	33	23	1,13	1,24	1,39	0,067	30	0,69	0,80	0,90	0,047
		OR5	18	8	1,20	1,29	1,43	0,067	13	0,75	0,83	0,92	0,048
	Cb	VR3	23	12	1,20	1,31	1,39	0,050	16	0,76	0,84	0,88	0,030
		VR1A	73	32	1,18	1,33	1,42	0,070	41	0,72	0,83	0,90	0,040
		VR4BB	31	24	1,21	1,32	1,42	0,060	28	0,80	0,85	0,90	0,030
		VR4B	7	6	1,24	1,31	1,36	0,040	6	0,76	0,84	0,89	0,040
		VR4A	40	26	1,25	1,33	1,44	0,050	36	0,79	0,84	0,92	0,040
		OR4A	9	4	1,32	1,37	1,43		6	0,82	0,86	0,92	0,040
	Ca	SR3	2	2	1,36		1,40		2	0,86		0,88	
		ART	148	103	1,19	1,30	1,39	0,044	124	0,76	0,84	0,92	0,034
m2	**Dd**	VA1A	32	17	1,04	1,10	1,19	0,040	18	0,86	0,92	0,99	0,040
		VA8A	7	6	0,97	1,00	1,04	0,020	7	0,77	0,83	0,89	0,050
		MOR3	1	1		0,99			1		0,77		
	Db	MOR2	1	1		1,01			1		0,90		
		FTE4	5	5	0,97	1,03	1,08	0,040	5	0,79	0,84	0,88	0,040
		COLD	58	47	0,98	1,03	1,12	0,040	56	0,79	0,86	0,91	0,030
		COLC	78	48	0,95	1,03	1,10	0,037	49	0,81	0,88	0,97	0,036
		COLB	6	4	0,96	1,00	1,06	0,042	4	0,82	0,84	0,86	
		VLT(a)	57	28	0,95	1,05	1,18	0,060	27	0,83	0,89	0,98	0,040
		VLT(b)	37	18	0,96	1,06	1,18	0,060	17	0,83	0,90	0,98	0,040
		VLT(c)	4	1		1,01			1		0,93		
	Da	VLT(d)	16	10	0,95	1,04	1,16	0,070	10	0,84	0,87	0,96	0,040
		FTE3	14	10	0,95	1,03	1,10	0,050	11	0,82	0,88	0,95	0,040
		FTE2	9	6	1,01	1,08	1,11	0,037	6	0,82	0,89	0,97	0,053
		OR9	29	26	0,96	1,02	1,07	0,040	29	0,77	0,84	0,89	0,030
		VR2B	16	12	0,98	1,05	1,12	0,050	13	0,83	0,89	0,97	0,040
		COLA	12	4	1,03	1,07	1,10		7	0,84	0,88	0,95	0,035
		VR2A	16	9	0,95	1,03	1,09	0,040	9	0,80	0,86	0,96	0,050
		OR8	42	29	0,94	1,02	1,10	0,045	38	0,74	0,83	0,90	0,044
		OR5	12	10	0,96	1,05	1,10	0,048	10	0,81	0,86	0,92	0,037
	Cb	VR3	30	21	0,98	1,04	1,14	0,040	24	0,82	0,87	0,95	0,040
		VR1A	75	46	0,94	1,03	1,14	0,050	50	0,78	0,86	0,96	0,040
		VR4BB	31	26	0,97	1,04	1,14	0,040	28	0,83	0,88	0,96	0,030
		VR4B	7	5	1,02	1,06	1,10	0,030	5	0,84	0,90	0,96	0,050
		VR4A	52	44	0,99	1,06	1,18	0,040	45	0,83	0,88	0,94	0,030
		OR4A	14	10	1,06	1,11	1,14	0,020	11	0,89	0,93	0,99	0,030
	Ca	SR3	3	2	1,09		1,14		1		0,97		
		ART	135	93	0,97	1,06	1,13	0,033	95	0,80	0,89	0,97	0,033
m3	**Dd**	VA1A	11	5	0,87	0,90	0,93	0,030	5	0,77	0,79	0,81	0,020
		FTE4	2	2	0,80		0,82		2	0,69		0,69	
	Db	COLD	2	2	0,84		0,89		2	0,74		0,78	
		COLC	7	6	0,78	0,84	0,92	0,050	7	0,71	0,76	0,88	0,059
		COLB	2	2	0,82		0,85		2	0,73		0,74	
		VLT(a)	22	12	0,77	0,84	0,93	0,050	15	0,63	0,73	0,87	0,050
	Da	VLT(b)	18	9	0,77	0,84	0,93	0,050	12	0,63	0,74	0,87	0,050
		VLT(c)	1	1		0,84			1		0,75		
		VLT(d)	3	3	0,82	0,85	0,89		3	0,66	0,70	0,72	
		VR2B	2	2	0,76		0,86		1		0,72		
		VR2A	2	2	0,81		0,85		1		0,70		
		OR8	6	6	0,76	0,84	0,90	0,048	6	0,67	0,71	0,74	0,024
		OR5	5	4	0,74	0,83	0,88		5	0,66	0,71	0,75	0,038
	Cb	VR1A	18	13	0,73	0,83	0,91	0,050	13	0,65	0,72	0,79	0,040
		VR4BB	6	4	0,86	0,89	0,91		4	0,73	0,76	0,80	
		VR4A	1	1		0,81			1		0,74		
		OR4A	5	3	0,87	0,91	0,94		4	0,73	0,74	0,76	
	Ca	ART	41	39	0,78	0,88	0,94	0,040	39	0,65	0,72	0,77	0,03

Table 4.2. Descriptive statistics of the lower molars of *Megacricetodon primitivus*. Abbreviations: LZ, Local zone; T.N., total number of teeth; N., number of teeth measured; min, minimum; max, maximum; δ, standard deviation. VLT (a), global measures of Valtorres (the three collections: type material + extra UU material + MNCN); VLT (b), Valtorres type material; VLT (c), Valtorres extra UU material; VLT (d), Valtorres MNCN. The measures of VR1A, OR5, OR8 and OR9 are from Daams and Freudenthal (1988a).

M2: The protolophule is anterior in 25 specimens, is anterior almost double in 12, is transverse in six, is transverse almost double in one, it is double in five and the entoloph is connected to the protocone indirectly through paracone and protolophule in one. In 16 out of 45 the ectoloph is strong, in 19 it is short and in 10 it is absent. A lingual mesocingulum that connects the protocone with the hypocone is present in six specimens (6/50). The mesoloph is long in eight, medium in 27, short in 12 and absent in two specimens. The ectoloph is connected with the mesoloph in seven, there is no connection between the ectoloph and the mesoloph in 29, there is a mesoloph but the ectoloph is absent in 10 and there is neither a mesoloph nor an ectoloph in two. The metalophule is anterior (25/45), transverse (7/45), points backwards and it is connected to the posteroloph, just behind the hypocone (9/45), the metalophule is more oblique reducing the posterosinus (3/45) or double (1/45).

M3: The lingual anterolophule is well developed in three, is incipient in four, and absent in eight. The protolophule is always anterior and the paracone is always well developed. The mesoloph is absent (5/18), incipient (2/18) or present (11/18). In one out of 18 the metalophule is absent, in three it is connected to the neo-entoloph, in eight the metalophule is connected to the anterior arm of the hypocone, in one the metalophule is connected to the neo-entoloph (or to the entoloph) and to the protolophule, in three the metalophule is connected to the anterior arm of the hypocone and the protolophule, and in two the metalophule is connected to the posterior arm of the protocone.

m1: The anteroconid is rounded and simple. Six out of 41 specimens have an antero-lingual cingulid. Only one specimen (1/43) has an antero-labial cingulid. A labial spur of the anterolophulid is present in three specimens and absent in 45. A short metalophulid spur is present in one specimen. The metalophulid is anteriorly connected in 42 specimens, is anteriorly connected with a second connection almost complete in seven, and is double in two. The lingual mesocingulid is present in 11 specimens, incipient in 22 and absent in 10. Only one specimen (1/47) has a mesostylid. The labial mesocingulid is present in 11, incipient in 10 and absent in 20. In two out of 43 there is an ectostylid. The mesolophid is medium (6/50), short (41/50) or absent (3/50). In two out of 53 there is an ectomesolophid. The hypolophulid is always anterior.

m2: The lingual anterolophulid is long in 12 specimens, short in 35 and absent in one. The lingual mesocingulid is present in 26, incipient in nine and absent in seven specimens. The mesostylid is usually absent (43/45). The labial mesocingulid is present in 11, incipient in 12 and absent in 15 specimens. Only one specimen (1/43) has an ectostylid. In six out of 51 the mesolophid is of medium length, in 37 it is short and in eight is absent. The hypolophulid is always anterior.

m3: The lingual anterolophulid is long in five specimens and short in the remaining 10. The labial mesocingulid is present (5/16), incipient (5/16) or absent (6/16). Two out of 17 have an ectostylid. The mesolophid is present in four specimens, incipient in one and absent in 15.

Evolutionary patterns of M. primitivus *from Calatayud-Montalbán Basin*

Near the type locality of Valtorres two other sites with *M. primitivus* have been found: Vilueña and Armantes 1A. The material from Vilueña has been assigned to *M. primitivus* by Sese, 2003. Despite the small amount of material, its size and morphology agree with the type material from Valtorres, and therefore we agree with this allotment.

The material from the locality of Armantes 1A (Daams et al., 1999c) is also very scarce (M1: 1.45 x 0.94; M2: 1.02 x 0.92; m2: >1.15 x >0.91). The upper molars (M1 and M2) agree with *M. primitivus* in size and morphology. The m2 is a corroded specimen. It is a larger than *M. primitivus*. Because the preservation of this specimen is poor and the morphology of m2 is poorly diagnostic in early *Megacricetodon* and *Democricetodon* , it could either be assigned to *Democricetodon franconicus* (and therefore correlated to local zone Da, as proposed by Daams et al., 1999c), or to *Megacricetodon vandermeuleni* (to local zone Db).

The assemblages attributed in this work to *M. primitivus* from the Aragonian Type Area and the Calamocha area show similar distribution of characters as the material from Valtorres (Appendix 4.1 Tab. 1 to 25). There are no clear evolutionary tendencies either in size or in morphology. The different assemblages show broad variability in the distribution of dental characters but are generally similar to that of the type material.

Finally, Freudenthal (1963) and Daams & Freudenthal (1988a) also included the material from the locality of Valdemoros 1A in *Megacricetodon primitivus*. This assemblage is similar in size to the type material of the species. However, we do not agree with the species assignment based on morphological differences. The material from VA1A differs from the material of *M. primitivus* from Valtorres, and the other localities included in our analysis, by the significantly higher percentage of the presence of an ectoloph in upper molars (Appendix 4.1 Tab. 6 and 13). In Valdemoros 1A the mesolophid is relatively shorter than in the *M. primitivus* samples studied (Appendix 4.1 Tab. 21). Furthermore, the observed differences between the assemblages of *M. primitivus* studied here and younger assemblages of *Megacricetodon* from Dc and Dd, are in our opinion, enough to reject a direct phylogenetic relationship, as was proposed by Daams & Freudenthal (1988a), representing *M. primitivus* a dead end on *Megacricetodon* evolution.

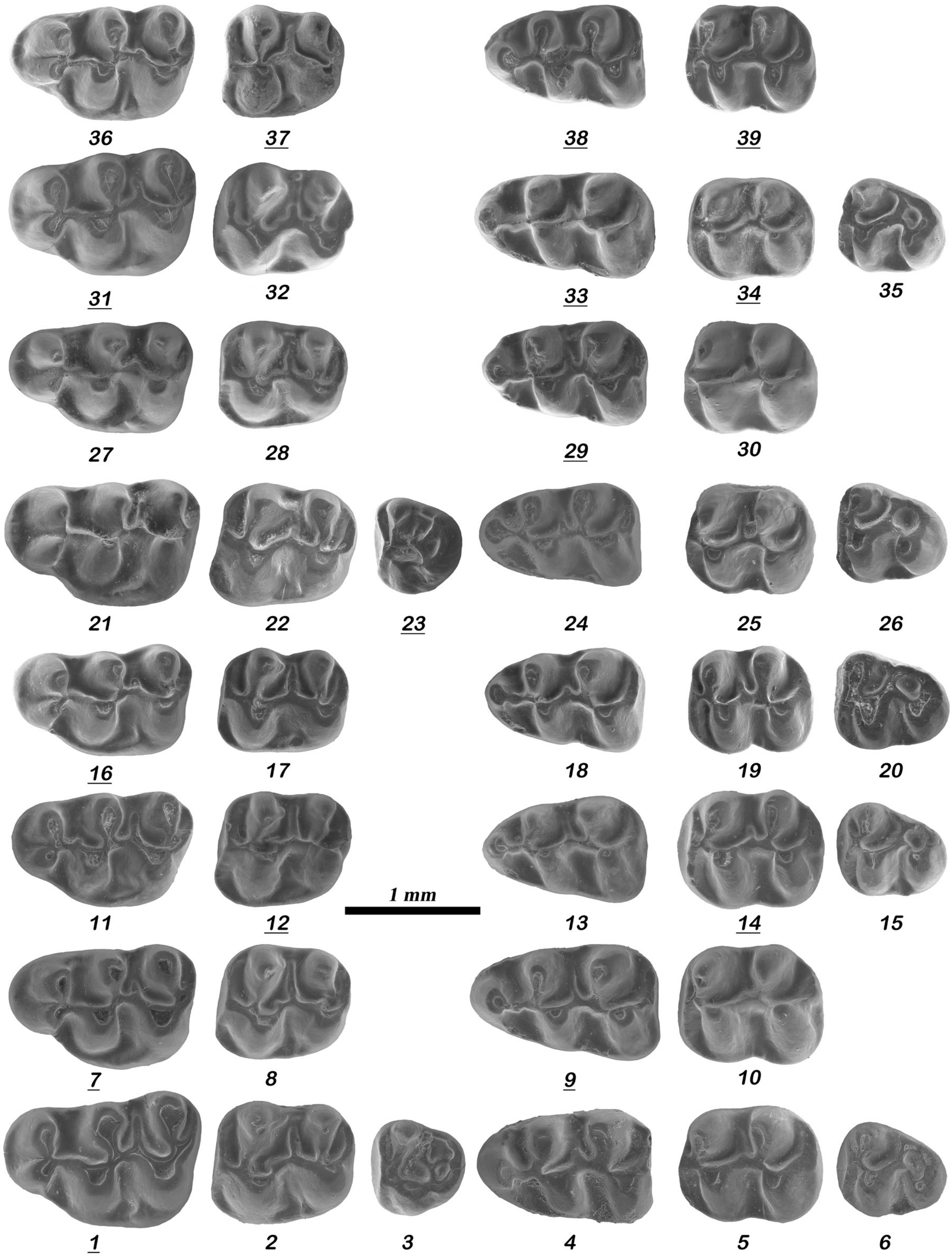


Figure 4.5. *Megacricetodon primitivus* from localities in the Calatayud-Montalbán Basin. Artesilla (Local zone Ca, approximately, 16. 5 Myr): 1, M1 ART-1417; 2, M2 ART-1450; 3, M3 ART-1.3; 4, m1 ART-1599; 5, m2 ART-1758; 6, m3 ART-3.2. Vargas 4BB (Local zone Cb, approximately, 16.120 Myr): 7, M1 VR4BB-1191; 8, M2 VR4BB-1203; 9, m1 VR4BB-1250; 10, m2 VR4BB-1270. Vargas 2A (Local zone Cb, approximately, 15.94 Myr): 11, M1 VR2A-23; 12, M2 VR2A-37; 13, m1 VR2A-46; 14, m2 VR2A-59; 15, m3 VR2A-67. La Col B (Local zone Da, approximately 15.88 Myr): 16, M1 COL-B-6; 17, M2 COL-B-16; 18, m1 COL-B-18; 19, m2 COL-B-21; 20, m3 COL-B-27. La Col C (Local zone Da, approximately 15.86 Myr): 21, M1 COL-C-2224; 22, M2 COL-C-2372; 23, M3 COL-C-2705; 24, m1 COL-C-2312; 25, m2 COL-C-2719; 26, m3 COL-C-2785. La Col D (Local zone Db, approximately 15.84 Myr): 27, M1 COL-D-171; 28, M2 COL-D-240; 29, m1 COL-D-334; 30, m2 COL-D-357. Fuente Sierra 4 (Local zone Db, approximately 15.82 Myr): 31, M1 FTE4-230; 32, M2 FTE4-233; 33, m1 FTE4-77; 34, m2 FTwE4-78; 35, m3 FTE4-426. Valdemoros 8A (Local zone Db, approximately 15.68 Myr): 36, M1 VA8A-505; 37, M2 VA8A-514; 38, m1 VA8A-520; 39, m2 VA8A-524. All of the teeth are at the same magnification. Scale bar equals 1 mm. Right side specimens underlined.

A more detailed comparison of this assemblage will be included on a revision of the *Megacricetodon* assemblages from younger localities correlated with local zones Dc and Dd (van der Meulen et al., 2012) and previously assigned by Daams & Freudenthal (1988a) to *M. collongensis*.

Megacricetodon primitivus is a stable species through time. Its morphology is conservative despite having great intra-populational variability (Appendix 4.1 Tab. 1-25). Since its first occurrence in the lower Aragonian (Ca) to its last occurrence in the middle Aragonian (Db), this species does not show any significant evolutionary trend in size (Table 4.1, 4.2) or in morphology. The most characteristic dental morphology is represented by the m1 with rounded anteroconid and short anterolophulid, and M1 with anterocone always double, with a small platform in front of the furrow and a strong lingual mesocingulum (Figure 4.5).

The stability in size and morphology which have *M. primitivus* contrasts with other species groups, such as the lineage *M. crusafonti-M. ibericus* from the Calatayud-Montalbán Basin, which show both increase in size and changes in morphology from its first occurrence in the upper Aragonian (local zone G2) to its last occurrence in the lower Vallesian (local zone H) (Daams & Freudenthal, 1988a). Other *Megacricetodon*, such as the German "*M. bavaricus* lineage", also shows a clear trend to increase its size and gradual changes in its morphology (Abdul- Aziz et al., 2010; Kälin & Kempf, 2009; Oliver & Peláez-Campomanes, 2013). The comparison among different regions suggests that the geographical variation of this species is also small, and therefore species could be recognized with a high degree of confidence.

But also other cricetids from the same time span and same basin show important changes through time: The lineage *Democricetodon decipiens-D. moralesi* (van der Meulen et al., 2003) have an increase of size and more derived morphology from the locality of Artesilla (approximately, 16. 5 Myr), to the locality of Valdemoros 8A (approximately 15.68 Myr), similar to what can be seen in Germany on the *M. bavaricus* lineage (Abdul Aziz et al., 2010; Oliver & Pelaez-Campomanes, 2013).

Therefore *M. primitivus* represent a rare example of evolutionary stasis among the different *Megacricetodon* lineages and its coeval taxa.

Megacricetodon primitivus *from other Spanish basins*

Levante basins*:* The *Megacricetodon* from Buñol (Valencia Basin) was assigned to *M. primitivus* (Adrover et al., 1987; Daams & Freudenthal, 1974). We agree with this allotment, based on the similar size and morphology shared by the material from Buñol and Valtorres.

The *Megacricetodon* from Araya and Mas de Antolino 2 (Ribesalbes-Alcora Basin) was assigned to *M. primitivus* by Agustí et al., (1988). Despite the small sample, both size and morphology allow us to assign them to this species.

Megacricetodon from the sites of Morteral 16, 17, 18, 19 and 11 (Rio Magro Basin) were assigned to *M. primitivus* by Ruiz-Sánchez et al., 2003. Based on the available information published (a few SEM photographs) it is not possible to decide on the taxonomic assignation of this material.

Loranca Basin: The *Megacricetodon* from Córcoles (Cuenca, Intermedia Depression) was allotted to *M. collongensis* by Díaz Molina & López Martínez (1979). The morphology and size of the material is compatible with its assignation to *M. primitivus* instead to *M. collongensis*. The new attribution is compatible with the proposed correlation of Corcoles to local zone C of the Calatayud-Montalbán Basin (Álvarez Sierra et al., 1994).

We have revised *Megacricetodon primitivus* from the locality of La Retama (Álvarez Sierra et al., 2006). Both, size and morphology agree with the *M. primitivus* from the Calatayud-Montalbán localities.

Vallés-Penedés Basin: *M. primitivus* is described in the localities of Can Martí Vell-1, Can Martí Vell-2, Can Julià-6 (Agustí, 1983), Casots-73 and Casots-74 (Agustí & Llenas, 1993). The only differences between the Catalonian *Megacricetodon* and the material from Valtorres are in material from the locality of Can Martí Vell-1, which has a protolophule and metalophule always anterior in the M2. Morphology and size of those samples agree with the populations of *M. primitivus* from Calatayud-Montalbán Basin.

Megacricetodon primitivus *from other European basins*

***Megacricetodon* from France**: During MN4 two species of *Megacricetodon* coexisted in France. Ginsburg & Bulot, 2000, indicated the presence of two *Megacricetodon* species in the localities of, Bézian, La Romieu Soucaret (La Romieu classique) and La Romieu Labadie (La Romieu supérieur). In addition, after studying the casts of the material from Pellecahus kindly lend by Dr. Pierre Mein, two species are also considered present. Bulot (1980) described the small species as *M. primitivus* in the site of Bézian. In the other Gers localities, the small form is assigned to either, *M.* aff. *collongensis,* or to *M.* cf. *collongensis* (Bulot, 1986, Ginsburg & Bulot, 2000). After the study of the more abundant material from the Calatayud Montalban basin, we think that the small forms from these Gers localities show morphologies that fit better with the general dental pattern of *M. primitivus* than to that of *M. collongensis* or contemporaneous forms.

***Megacricetodon* from Portugal**: *Megacricetodon primitivus* is described from Quinta das Pedreiras and Quinta do Pombeiro in the Va_2 unit, MN4 (Antunes, 1984; Mein, 2000), and from Charneca do Lumiar, Quinta de Farinheira and Chelas 1 in the lower part of the Vb unit, MN5 (Pais et al., 2012). Whereas, *M. collongensis* occurs in the sites of Chelas 2, Quintanelas and Amor, representing the upper part of the Vb (MN 5, Pais et al., 2012). The correlation between the Lisbon Miocene units (Cotter, 1956) with the Calatayud-Montalbán Basin and the Spanish local zones (Antunes, 1984, 2000; Antunes et al., 1987; Antunes et al., 1996; Antunes et al., 1999; Mein, 2000, Pais et al., 2012) is straightforward. Vb unit has been correlated to zone D of Calatayud-Montalbán basin; the lower part of Vb to Da-Db and the upper part to Dc-Dd (Mein, 2000; Pais et al., 2012). We have not studied the material but according to the published information we interpret that *M. primitivus* was also present in western Iberian Peninsula, and with a similar temporal distribution.

***Megacricetodon* from Greece**: The locality of Aliveri is situated in the island of Evia (Álvarez Sierra et al., 1987; Benda & De Bruijn, 1982; De Bruijn et al., 1980; Katsikatsos et al., 1981). Hofmeijer & De Bruijn (1988) studied the cricetids from Aliveri. They assign the *Megacricetodon* material to *M. primitivus*, despite the observation of several dental characteristics differentiating the material from those localities. They indicated that *Megacricetodon* from Aliveri is more primitive than *M. primitivus* from Valtorres, suggesting the earlier appearance of *Megacricetodon* in the East Mediterranean area than in the Western area. In our opinion, *Megacricetodon* from Aliveri (specially the North Quarry) differs from *M. primitivus* by: the slightly split anterocone of the M1, the higher percentage of metalophulid double in the m1, and the higher percentage of mesolphids in the m3. The size is similar except for the upper/lower m3 (in the North Quarry), which are bigger.

Vasileiadou & Koufos (2005) indicated that *Megacricetodon* from Antonios (Chalkidiki, North Greece) shows many similarities with *Megacricetodon* from Aliveri and assigned this material to *M. primitivus*. Comparing these fossils to the Spanish *M. primitivus* we noticed some differences such as the anteroconid always simple and slightly elongated; the shorter mesolophid of the m1 (short (6/12) or absent (6/12)); the M1 always has a cingulum ridge in front of the anterocone and always has a short ectoloph. Moreover, the size is slightly bigger.

Based on these results, we think that the *Megacricetodon* from those Greek localities represent a new species different from *M. primitivus*.

***Megacricetodon* from Turkey**: The *Megacricetodon* material from Turkish localities correlated to MN3 to MN5 have being assigned to *Megacricetodon* sp. (Kaya et al., 2007; Wessels, 2009), *M.* cf. *primitivus* (Ünay & Göktas, 1999, 2000), *M. primitivus*

(Ünay & Göktas, 1999, Alçiçek, 2010), *M. collongensis* (De Bruijn et al., 2003, Ünay et al., 2003; Mazzini et al., 2013), and *M.* cf. *collongensis* (Kaya et al., 2007). We have not studied this material since is under study by Turkish colleagues. Therefore, new information will probably improve the knowledge on the evolution and distribution of *Megacricetodon* in the Anatolian region and the early migrations of the genus into Europe.

4.6. BIOSTRATIGRAPHIC CONSIDERATIONS

The site of Valtorres is located in the Calatayud-Montalbán Basin, in the Iberian Range (NE of the Iberian Peninsula). Freudenthal and De Bruijn were the first to start a systematic research on rodents from this basin. De Bruijn centered his research in the Gliridae, Sciuridae and Eomyidae of this area (De Bruijn, 1967); whereas Freudenthal (1963) studied the Cricetidae.

The locality of Valtorres is divided to two fossiliferous layers: Layer A is a grey, sandy clay which only contains macromammals: *Cainotherium miocenicum*, *Anchitherium* sp., *Rhinoceros* sp., *Palaeomeryx* sp., Cervidae sp. and *Trilophodon* sp.). And layer B is a red clay with large and small mammals: *Cainotherium miocenicum*, *Lagopsis penai*, *Simplomys simplicidens*, *Microdyromys koenigswaldi*, *Heteroxerus rubricati*, *Atlantoxerus blacki*, *Democricetodon koenigswaldi* and *Megacricetodon primitivus*.

Initially, the site of Valtorres was correlated by Daams & Freudenthal (1988b) with Olmo Redondo 9 and Valdemoros 1A (local zone D1). The biostratigraphy proposed by Daams & Freudenthal (1988b) was corrected by Daams et al., (1999a) and van der Meulen et al*.,* (2012). In this new biostratigraphy Olmo Redondo 9 correlates with local zone Da, while Valdemoros 1A to local zone Dd. The unambiguous correlation of Valtorres with the Aragonian type area is complicated due to the lack of magnetostratigraphic data. The scarce material of *Democricetodon* and the wide stratigraphical distribution of other small mammals (*Atlantoxerus blacki*, *Heteroxerus rubricati*, *Simplomys simplicidens*, *Microdyromys koenigswaldi*, *Lagopsis penai*) do not help in correlation. *Atlantoxerus blacki* can be used to determine the possible youngest age for Valtorres since its upper record is in local zone Dc (Peláez-Campomanes, 2000; van der Meulen et al*.,* 2012). In addition, the differences observed between the *Megacricetodon* material from Valtorres and Valdemoros 1A indicate that a correlation of the former with local zone Dd is not suitable. *Megacricetodon* allows us to refine the age of the locality: The absence in Valtorres of *Ligerimys* (Eomyidae) excludes the correlation to the MN4 (local zone Ca and Cb). The absence of *M. vandermeuleni* excludes the correlation to zone Db. On the other hand, Valtorres and Armantes 1A (Daams et al., 1999c) are located lower stratigraphically than Munébrega I and III (De Bruijn, 1967). These localities are correlated with local zone Dc (middle Miocene), based on the occurrence of *Democricetodon jordensi* and a form of *Megacricetodon* larger than *M.*

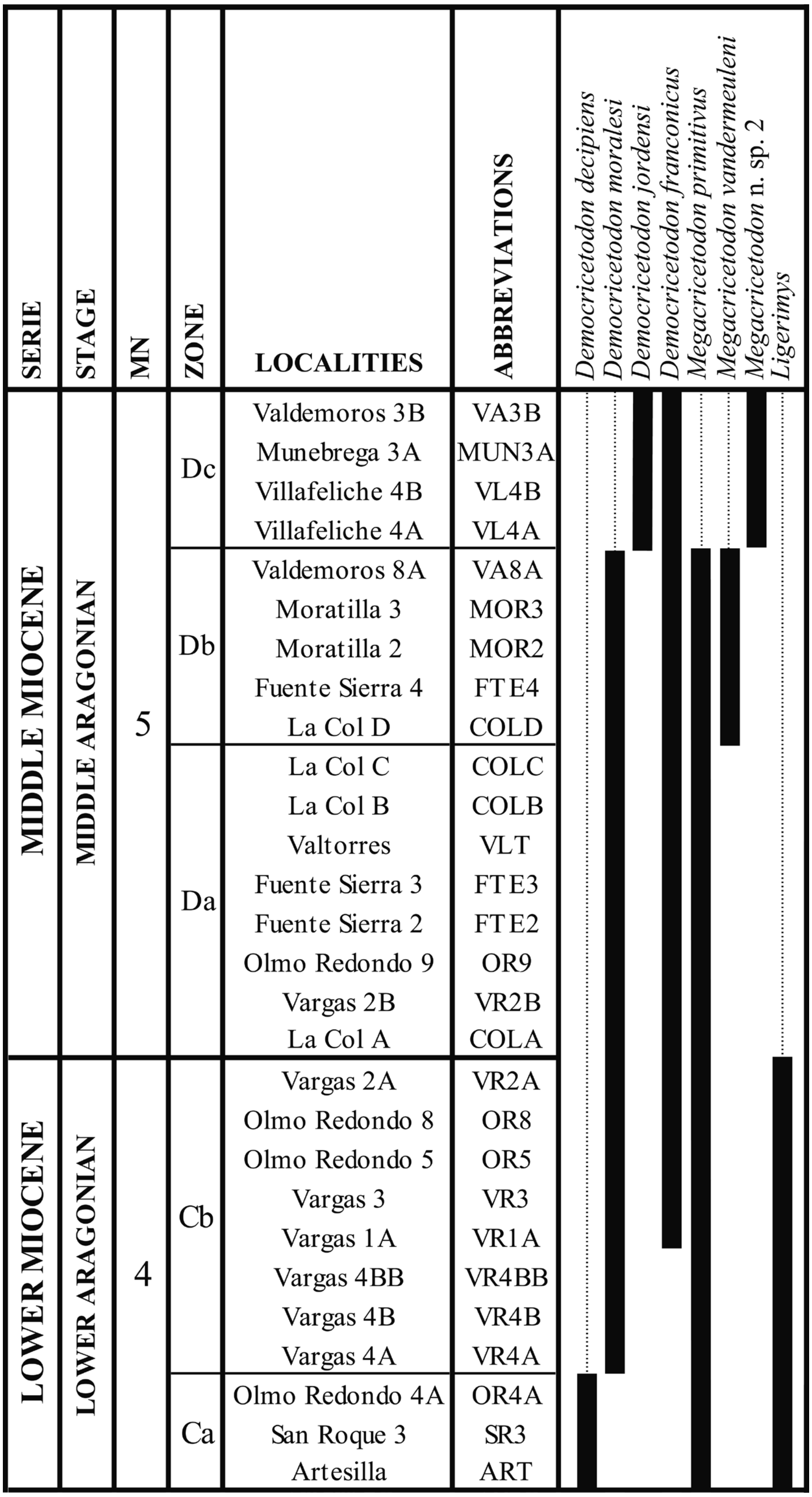


Figure 4.6. Distribution range of key taxa from the Calatayud-Montalbán Basin, used in the bioestratigraphical correlations (after van der Meulen et al., 2012 and Oliver & Peláez-Campomanes, 2013).

primitivus and named as *Megacricetodon* n. sp. 2 by van der Meulen et al., (2012). Therefore, we conclude that the assemblage from Valtorres can be correlated to local zone Da, middle Aragonian (see Figure 4.6).

Based on the studied material the stratigraphic distribution of *M. primitivus* is from local zone Ca (locality of Artesilla, approximately, 16. 5 Myr), to local zone Db (locality of Valdemoros 8A, approximately 15.68 Myr). This stratigraphical distribution of *M. primitivus* in the Calatayud-Montalbán Basin is compatible with that observed in other Spanish basins, as well as in Portuguese and French basins.

4.7. CONCLUSIONS

We have restudied and described the type material of *M. primitivus,* as well as new undescribed material, from the locality of Valtorres (Calatayud-Montalbán Basin). Valtorres is an unusual site where the fossils show strong deformation and fractures. The taphonomical processes have affected specially the dental size, causing overestimation or underestimation of the measurements of strongly affected teeth. The age of the locality has been discussed and a middle Miocene age (local zone Da) has been proposed.

We have also study other populations of *M. primitivus* from the Calatayud-Montalbán Basin since its occurrence in the lower Aragonian (local zone Ca) to its last occurrence in the middle Aragonian (local zone Db).

The evolutionary patterns of this species show a very conservative morphology and size, despite the morphologic characteristics have high intra-populational variability.

After the study of other European population of *Megacricetodon* assigned to *M. primitivus*, we can conclude that the geographical distribution of *M. primitivus* is restricted to the Iberian Peninsula and France (Southwest of Europe). All other assemblages described as *M. primitivus* outside this area show enough morphological differences to be considered as different taxa.

4.8. REFERENCES

Abdul Aziz, H., M. Böhme, A. Rocholl, J. Prieto, J. R. Wijbrans, V. Bachtadse, and A. Ulbig. 2010. Integrated stratigraphy and 40Ar/39Ar chronology of the Early to Middle Miocene Upper Freshwater Molasse in western Bavaria (Germany). International Journal of Earth Sciences 99:1859-1886.

Adrover, R., P. Mein, and M. Belinchon. 1987. La fauna de roedores en el Aragoniense medio del Barranco del Candel, Buñol (provincia de Valencia, España). Paleontologia i Evolucio 21:43-61.

Aguilar, J. P. 1995. Evolution de la lignée *Megacricetodon collongensis-Megacricetodon rousillonensis* (Cricetidae, Rodentia, Mammalia) au cours du Miocène inférieur et moyen dans le sud de la France. Palaeovertebrata 24:1-45.

Agustí, J. 1983. Roedores (Mam.) del Mioceno inferior de Can Marti Vell (Vallès-Penedès, Cataluña, España). Estudios Geologicos. Madrid 39:417-430.

Agustí, J., P. Anadón, L. Ginsburg, P. Mein, and P. Moissenet. 1988. Araya et Mira: nouveaux gisements de mammifères dans le Miocène inférieur-moyen des chaînes Ibériques orientales et méditerranéennes. Conséquences stratigraphiques et structurales. Paleontologia i Evolucio 22:83-101.

Agustí, J., and M. Llenas. 1993. Los roedores del Mioceno Inferior de Els Casots (Vallés-Penedés). Nota preliminar. Comunicaciones de las IX Jornadas de Paleontología, Málaga:70-72.

Alcicek, H. 2010. Stratigraphic correlation of the Neogene basins in southwestern Anatolia: Regional palaeogeographical, palaeoclimatic and tectonic implications. Palaeogeogr Palaeoclimatol Palaeoecol 291:297-318.

Alvarez-Sierra, M. A., and E. García-Moreno. 1986. New Gliridae and Cricetidae from the Middle and Upper Miocene of the Duero Basin, Spain. Studia Geologica Salmanticensia 22:145-189.

Álvarez Sierra, M. A., R. Daams, and P. Peláez-Campomanes. 1994: Synthesis of Late Oligocene/Early Miocene micromammal faunas of the Loranca Basin (Province of Cuenca, Spain). Paper presented at the Comunicaciones de las X Jornadas de Paleontología, Madrid, 1994.

Álvarez Sierra, M. A., R. Daams, and A. J. Van der Meulen. 1987. The mammals from the lower Miocene of Aliveri (island of Evia, Greece). VII. The Eomyidae. Proceedings of the Koninklijke Nederlandse Akademie Van Wetenshappen 90:47-56.

Álvarez Sierra, M. A., I. García Paredes, L. W. van den Hoek Ostende, A. J. van der Meulen, P. Peláez-Campomanes, and P. Sevilla. 2006. The Middle Aragonian (Middle Miocene) Micromammals from La Retama (Intermediate Depression, Tagus Basin) Province of Cuenca, Spain. Estudios Geológicos 62:401-428.

Antunes, M. T. 1984. Essai de synthèse sur les Mammifères du Miocène de Portugal. Volume d'hommage au géologue G. Zbyszewski. Recherche sur les civilisations:301-323.

Antunes, M. T. 2000. Miocene mammals from Lisbon and geologic age. A showcase for marine-continental correlations. Ciências da Terra (UNL) 14:343-348.

Antunes, M. T., J. P. Calvo Sorando, M. Hoyos, J. Morales, S. Ordóñez, F. J. Pais Pais, and C. Sesé. 1987. Ensayo de Correlación Entre el Neógeno de las Áreas de Madrid y Lisboa (Cuencas Alta y Baja del Rio Tajo). Comunicaçoes dos Serviços Geológicos de Portugal 73:85-102.

Antunes, M. T., P. Legoinha, A. Nascimento, and J. Pais. 1996. The evolution of the Lower Tagus basin (Lisbon and Setubal Peninsula, Portugal) from Lower to early Middle Miocene. Geologie de la France 4:59-77.

Antunes, M. T., J. Pais, A. Balbino, P. Mein, and J.-P. Aguilar. 1999. The Cristo Rei section (Lower Miocene) Distal fluviatile environments in a marine series, plants, vertebrates and other evidence, age. Ciencias da Terra (UNL9 13:141-155.

Benda, L., and H. de Bruijn. 1982. Biostratigraphic correlations in the Eastern Mediterranean Neogene. 7. Calibration of sporomorph-and rodent-association in the Aliveri-Kymi basin, Island of Euboea (Greece). Newsletters on Stratigraphy 11:128-135.

Bi, S., J. Meng, and W. Wu. 2008. A new species of *Megacricetodon* (Cricetidae, Rodentia, Mammalia) from the Middle Miocene of northern Junggar Basin, China. American Museum Novitates 3602:1-23.

Bowdich, T. E. 1821. An Analysis of the Natural Classification of Mamalia for the Use of Students and Travellers. 115 pp. Smith, J., Paris.

Bruijn, d. H., L. W. van den Hoek Ostende, M. R. Kristkoiz-Boon, K. Theocharapoulos, and E. Ünay. 2003. Rodents, lagomorphs and insectivores, from the middle Miocene hominoid locality of Çandir (Turkey). Courier Forschungsinstitut Senckenberg 240:51-87.

Bruijn, H., de. 1967. Gliridae, Sciuridae y Eomyidae (Rod.Mam.) Miocenos de Calatayud (provincia de Zaragoza, Espana) y su relacion con la biosetratigrafia del area, pp. 187. Utrecht.

Bruijn, H. d., A. J. Meulen, van der, and G. Katsikatsos. 1980. The mammals from the lower Miocene of Aliveri (Island of Evia, Greece) 1. The Sciuridae. Proceedings of the Koninklijke Nederlandse Akademie Van Wetenshappen, sér. B 83:241-261.

Bulot, C. 1980. Nouvelle description de deux especes du genre *Megacricetodon* (Cricetidae, Rodentia) du Miocene de Bezian (Zone de La Romieu). Bulletin du Museum National d'Histoire Naturelle Section C Sciences de la Terre Paleontologie Geologie Mineralogie 2:3-16.

Bulot, C. 1986. Distinction de deux niveaux fossilifères dans le gisement traditionnel de La Romieu (Gers). Bulletin du Muséum d'Histoire Naturelle. Sciences de la Terre. Paris, 4ème sér. 8:483-497.

Cotter, J. C. B. 1956. O Miocénico marinho de Lisboa: In *Comunicaçoes dos Serviços Geológicos de Portugal*, Vol. 36, pp. 1-170, Lisboa.

Daams, R., L. Alcalá, M. A. Alvarez Sierra, B. Azanza, J. A. van Dam, A. J. van der Meulen, J. Morales, M. Nieto, P. Peláez-Campomanes, and D. Soria. 1998. A stratigraphical framework for Miocene (MN4-MN13) continental sediments of central Spain. Comptes Rendus de l'Academie des Sciences, Serie II. Sciences de la Terre et des Planetes 327:625-631.

Daams, R., and M. Freudenthal. 1974. Early Miocene Cricetidae (Rod. Mam.) from Buñol (province of Valencia, Spain). Scripta Geologica 24:1-19.

Daams, R., and M. Freudenthal. 1988a. Cricetidae (Rodentia) from the type-Aragonian; the genus Megacricetodon; pp. 39-132 *in* M. Freudenthal (ed.), Biostratigraphy and paleoecology of the Neogene micromammalian faunas from the Calatayud-Teruel Basin (Spain). Scripta Geologica, Special Issue 1, Leiden.

Daams, R., and M. Freudenthal. 1988b. Synopsis of the Dutch-Spanish collaboration program in the Neogene of the Calatayud-Teruel basin; pp. 3-18 *in* M. Freudenthal (ed.), Biostratigraphy and paleoecology of the Neogene micromammalian faunas from the Calatayud-Teruel Basin (Spain). Scripta Geologica, Special Issue 1, Leiden.

Daams, R., A. J. v. d. Meulen, P. Peláez-Campomanes, and M. A. Álvarez Sierra. 1999a. Trends in rodent assemblages from the Aragonian (early-middle Miocene) of the Calatayud-Daroca Basin, Aragón, Spain.; pp. 127-139 *in* J. Agustí, L. Rook, and P.

Andrews (eds.), Hominoid evolution and climatic change in Europe. Cambridge University Press, Cambridge.

Daams, R., A. J. van der Meulen, M. A. Álvarez-Sierra, P. Peláez-Campomanes, J. P. Calvo, M. A. Alonso Zarza, and W. Krijgsman. 1999b. Stratigraphy and sedimentology of the Aragonian (Early to Middle Miocene) in its type area (North-Central Spain). Newsletters on Stratigraphy 37:103-139.

Daams, R., A. J. van der Meulen, M. A. Álvarez-Sierra, P. Peláez-Campomanes, and W. Krijgsman. 1999c. Aragonian stratigraphy reconsidered, and a re-evaluation of the middle Miocene mammal biochronology in Europe. Earth and Planetary Science Letters 165:287-294.

Daxner, G. 1967. Ein neuer cricetodontide (Rodentia, Mammalia) aus dem Pannon des Wiener Beckens. Annalen des Naturhistorischen Museums in Wien 71:27-36.

Díaz Molina, M., and N. López Martínez. 1979. Terciario continental de la Depresión Intermedia (Cuenca). Bioestratigrafía y Paleogeografía. Estudios Geológicos 35:149-167.

Erten, H., S. Sen, and M. Gormus. 2014. Middle and Late Miocene Cricetidae (Rodentia, Mammalia) from Denizli Basin (Southwestern Turkey) and a new species of *Megacricetodon*. Journal of Paleontology 88:504-518.

Fahlbusch, V. 1964. Die Cricetiden (Mam.) der Oberen Süsswasser-Molasse Bayerns. Bayerische Akademie Wissenschaften. Mathematisch-naturwissenschaftliche Klasse. Munchen 118:1-135.

Freudenthal, M. 1963. Entwicklungsstufen der Miozänen Cricetodontinae (Mam. Rod.). In *Mittelspaniens und ihre Stratigraphische Bedeutung*, pp. 107. Ricks University, Utrecht.

Freudenthal, M. 1968. On the mammalian fauna of the *Hipparion* beds in the Calatayud-Teruel basin Part IV: The genus *Megacricetodon* (Rod.). Proceedings of the Koninklijke Nederlandse Akademie Van Wetenschappen, sér. B 71:57-72.

Ginsburg, L., and C. Bulot. 2000. Le cadre stratigraphique du site de Sansan. Memoires du Museum National d'Histoire Naturelle 183:39-67.

Heissig, K. 1990. The faunal succession of the Bavarian Molasse reconsidered - Correlation of the MN 5 and MN 6 faunas; pp. 181-192 *in* E. H. Lindsay, V. Fahlbusch, and P. Mein (eds.), European Neogene Mammal Chronology. Plenum Press NATO ASI New York-London.

Heissig, K. 1997: Mammal faunas intermediate between the reference faunas of MN 4 and MN 6 from the Upper Freshwater Molasse of Bavaria. Paper presented at the Actes du Congrès BiochroM'97, Montpellier, 1997.

Kälin, D., and O. Kempf. 2009. High-resolution stratigraphy from the continental record of the Middle Miocene Northern Alpine Foreland Basin of Switzerland. Neues Jahrbuch Fur Geologie Und Palaontologie-Abhandlungen 254:177-235.

Katsikatsos, G., H. d. Bruijn, and A. J. v. d. Meulen. 1981. The Neogene of the Island of Euboea (Evia), a review. Geologie en Mijnbouw:509-516.

Kaya, O., E. Ünay, F. Göktas, and G. Sarac. 2007. Early Miocene stratigraphy of central west Anatolia, Turkey: implications for the tectonic evolution of the eastern Aegean area. Geological Journal 42:85-109.

Klein Hofmeijer, G., and H. Bruijn, de. 1988. The mammals from the lower Miocene of Aliveri (Island of Evia, Greece)Part 8: The Cricetidae. Proceedings of the Koninklijke Nederlandse Akademie Van Wetenshappen, sér. B 91:185-204.

Lartet, E. 1851. Notice sur la colline de Sansan. Portes, Auch:1-47.

Lazzari, V., and J. P. Aguilar. 2007. Les *Megacricetodon* du gisement karstique miocène moyen de Blanquatère 1 (Pyrénées-Orientales, Sud de la France): nouvelles espèces, implications biochronologique et phylogénetique. Geobios 40:91-111.

Lindsay, E. H. 1988. Cricetid rodents from Siwalik deposits near Chinji Village: part 1: Megacricetodontinae, Myocridetontinae and Dendromurinae. Paleovertebrata 18:95-154.

Maridet, O., W.-Y. Wu, J. Ye, S.-D. Bi, X.-J. Ni, and J. Meng. 2011. Early Miocene cricetids (Rodentia) from the Junggar basin (Xinjiang, China) and their biochronological implications. Geobios (Villeurbanne) 44.

Mazzini, I., N. Hudackova, P. Joniak, M. Kovacova, T. Mikes, A. Mulch, B. Rojay, S. Lucifora, D. Esu, and I. Soulie-Marsche. 2013. Palaeoenvironmental and chronological constraints on the Tuglu Formation (Çankiri Basin, Central Anatolia, Turkey). Turkish J Earth Sci 22:1-31.

Mein, P. 1958. Les mammifères de la faune sidérolithique du Vieux -Collonges. Nouvelles Archives du Muséum d'Histoire Naturelle de Lyon 5:1-122.

Mein, P. 2000. La biochronologie des mammifères néogènes d'Europe. L'échelle MN, son application à la succession des faunes du Portugal. Ciências da Terra (UNL) 14:335-342.

Oliver, A., I. García-Paredes, and P. Pelaez-Campomanes. 2009a. A geometric morphometric analysis of *Megacricetodon* (Cricetodontinae, Rodentia, Mammalia) from the Db Biozone, Middle Aragonian. Paleontologia i Evolucio Memòria especial 3:101-102.

Oliver, A., P. López-Guerrero, I. García-Paredes, M. A. Álvarez Sierra, and P. Pelaez-Campomanes. 2009b. Evolution of *Megacricetodon* tooth pattern through geometric morphometrics analysis. Journal of Vertebrate Paleontology 29:158A.

Oliver, A., and P. Pelaez-Campomanes. 2013. *Megacricetodon vandermeuleni,* sp. nov. (Rodentia, Mammalia), from the Spanish Miocene: a new evolutionary framework for Megacricetodon. Journal of Vertebrate Paleontology 33:943-955.

Oliver Pérez, A., P. López-guerrero, and P. Pelaez-Campomanes. 2008. Primer representante del género *Megacricetodon* de la Cuenca de Calatayud-Daroca (Zaragoza, España); pp. 317-329 *in* J. Esteve, and G. Meléndez (eds.), Palaeontológica Nova. Publicaciones del Seminario de Paleontología de Zaragoza, Zaragoza.

Pais, J., P. P. Pedro P. Cunha, D. Pereira, P. Legoinha, R. Dias, D. Moura, A. B. da Silveira, J. C. Kullberg, and J. A. González-Delgado. 2012. The Paleogene and Neogene of Western Iberia (Portugal): A Cenozoic Record in the European Atlantic Domain; pp. 1-138 *in* J. Pais (ed.), The Paleogene and Neogene of Western Iberia (Portugal)A Cenozoic record in the European Atlantic domain. SpringerBriefs in Earth Sciences, Berlin Heidelberg.

Peláez-Campomanes, P. 2000. Mammalian faunas from the paleogene of the Sierra Palomera (Teruel, Spain). Journal of Paleontology 74:336-348.

Peláez-Campomanes, P., and R. Daams. 2002. Middle Miocene rodents from Pasalar, Anatolia, Turkey. Acta Palaeontologica Polonica 47:125-132.

Qiu, Z. 1996. Middle Miocene micromammals faunas from Tunggur, Nei, Mongolia. 216 pp. Beijing Science Press.

Qiu, Z., C. Li, and S. Wang. 1981. Miocene mammalian fossils from Xining Basin, Qinghai. Vertebrata Palasiatica 19:156-173.

Radulescu, C., and P. Samson. 1988. Les cricetides (Rodentia, Mammalia) du Miocene (Astaracien superieur) de Roumanie. Travaux de l'Institut de Speologie "Emile Racovitza" 27:67-78.

Ruiz-Sánchez, F. J., C. de Santiesteban Bové, and J. I. Lacomba Andueza. 2003. Nuevas faunas de roedores fósiles (Mammalia, Rodentia) de edad Aragoniense inferior y medio en la serie del Barranco Morteral (cuenca del Río Magro, prov. de Valencia, España). Coloquios de Paleontología Volumen Extraordinario I:579-594.

Sesé, C. 2003. Paleontología y bioestratigrafía del Mioceno continental de la Cuenca de Calatayud (Zaragoza): Nuevos yacimientos de micromamíferos. Estudios Geológicos 59:249-264.

Ünay, E., d. H. Bruijn, and G. Sarac. 2003. A preliminar zonation of the continental Neogene of Anatolia based on rodents; pp. 539-547 *in* J. W. F. Reumer, and W. Wessels (eds.), Distribution and migration of tertiary mammals in Eurasia. A volume in honour of Hans de Bruijn. Deinsea 10.

Ünay, E., and F. Göktas. 1999. Late Early Miocene and Quaternary small mammals in the surroundings of Söke (Aydm): Preliminary results. Geological Bulletin of Turkey 42:99-113.

Ünay, E., and F. Göktas. 2000. Small Mammal Biochronology of the Early Miocene Lignitiferous Sediments Around Kýnýk (Gördes): Preliminary Results. Geological Bulletin of Turkey 43:1-5.

van der Meulen, A. J., I. García-Paredes, M. A. Álvarez-Sierra, L. W. van den Hoek Ostende, K. Hordijk, A. Oliver, and P. Peláez-Campomanes. 2012. Updated Aragonian biostratigraphy: Small Mammal distribution and its implications for the Miocene European Chronology. Geologica Acta 10:159-179.

van der Meulen, A. J., P. Peláez-Campomanes, and R. Daams. 2003. Revision of medium-sized Cricetidae from the Miocene of the Daroca-Villafeliche area in the Calatayud-Teruel basin (Zaragoza, Spain). Coloquios de Paleontología Volumen Extraordinario 1:385-441.

van der Meulen, A. J., P. Peláez-Campomanes, and S. A. Levin. 2005. Age structure, residents, and transients of Miocene rodent communities. American Naturalist 165:108-125.

Vasileiadou, K., and G. D. Koufos. 2005. The micromammals from the Early/Middle Miocene locality of Antonios, Chalkidiki, Greece. Annales de Paleontologie 91:197-225.

Wessels, W. 2009. Miocene rodent evolution and migration: Muroidea from Pakistan, Turkey and Northern Africa: In *Geologica Ultraiectina*, Vol. 307, pp. 1-290.

APPENDIX 4.1

DISTRIBUTION OF CHARACTER STATES

Table 1. Anterocone M1

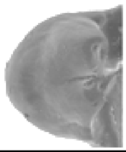
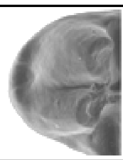
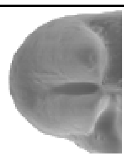
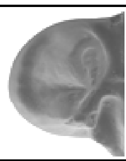
Localities						N
Valdemoros 1A		2 (9%)	2 (9%)	16 (70%)	3 (13%)	23
Valdemoros 8A		4 (44%)		4 (44%)	1 (11%)	9
Moratilla 3				1 (50%)	1 (50%)	2
Moratilla 2		1 (33%)		2 (67%)		3
Fuente Sierra 4			3 (50%)	3 (50%)		6
La Retama	1 (2%)	7 (12%)	6 (10%)	23 (38%)	23 (38%)	60
La Col-D		1 (3%)	6 (15%)	25 (63%)	8 (20%)	40
La Col-C		3 (5%)	9 (15%)	44 (72%)	5 (8%)	61
La Col-B			1 (13%)	7 (88%)		8
Valtorres (type material+MNCN)		3 (7%)	18 (40%)	21 (47%)	3 (7%)	45
Valtorres type Material			15 (63%)	7 (29%)	2 (8%)	24
Valtorres extra type Material		1 (10%)	1 (10%)	8 (80%)		10
Valtorres MNCN		2 (18%)	2 (18%)	6 (55%)	1 (9%)	11
Fuente Sierra 3		1 (17%)	2 (33%)	3 (50%)		6
Fuente Sierra 2			1 (33%)	2 (67%)		3
Vargas 2B		1 (11%)	2 (22%)	3 (33%)	3 (33%)	9
Olmo Redondo 9		1 (5%)	3 (14%)	14 (67%)	3 (14%)	21
La Col-A			2 (40%)	3 (60%)		5
Vargas 2A				4 (100%)		4
Olmo Redondo 8		4 (20%)	3 (15%)	10 (50%)	3 (15%)	20
Olmo Redondo 5			1 (9%)	9 (82%)	1 (9%)	11
Vargas 3	1 (6%)	4 (25%)	7 (44%)	4 (25%)		16
Vargas 1A	4 (9%)	5 (11%)	9 (20%)	25 (57%)	1 (2%)	44
Vargas 4BB			6 (24%)	16 (64%)	3 (12%)	25
Vargas 4B		1 (25%)	3 (75%)			4
Vargas 4A	2 (7%)	3 (10%)	6 (20%)	18 (60%)	1 (3%)	30
Olmo Redondo 4A		2 (18%)		9 (82%)		11
San Roque 3		2 (50%)		2 (100%)		4
Artesilla	4 (4%)	12 (13%)	28 (29%)	49 (52%)	2 (2%)	95

Table 2. Symmetry of the Anterocone M1

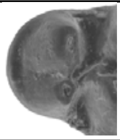
Localities				N
Valdemoros 1A	6 (23%)	18 (69%)	2 (8%)	26
Valdemoros 8A	1 (10%)	9 (90%)		10
Moratilla 3		1 (100%)		1
Moratilla 2	1 (25%)	3 (75%)		4
Fuente Sierra 4	6 (100%)			6
La Retama	7 (10%)	66 (90%)		73
La Col-D	4 (9%)	41 (91%)		45
La Col-C	7 (10%)	59 (88%)	1 (1%)	67
La Col-B		8 (100%)		8
Valtorres (type material+MNCN)	9 (20%)	36 (80%)		45
Valtorres type Material	6 (26%)	17 (74%)		23
Valtorres extra type Material	1 (10%)	9 (90%)		10
Valtorres MNCN	2 (17%)	10 (83%)		12
Fuente Sierra 3	1 (14%)	6 (86%)		7
Fuente Sierra 2	1 (25%)	3 (75%)		4
Vargas 2B	1 (11%)	8 (89%)		9
Olmo Redondo 9	2 (8%)	23 (92%)		25
La Col-A	1 (20%)	4 (80%)		5
Vargas 2A		4 (100%)		4
Olmo Redondo 8	1 (5%)	21 (95%)		22
Olmo Redondo 5	1 (8%)	11 (92%)		12
Vargas 3	2 (13%)	14 (88%)		16
Vargas 1A	3 (6%)	49 (94%)		52
Vargas 4BB	3 (13%)	21 (88%)		24
Vargas 4B	1 (25%)	3 (75%)		4
Vargas 4A	10 (33%)	20 (67%)		30
Olmo Redondo 4A	2 (18%)	9 (82%)		11
San Roque 3		4 (100%)		4
Artesilla	47 (46%)	56 (54%)		103

Table 3. Anterolophule M1

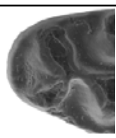
Localities				N
Valdemoros 1A	14 (50%)	14 (50%)		28
Valdemoros 8A	8 (73%)	3 (27%)		11
Moratilla 3	3 (100%)			3
Moratilla 2	5 (100%)			5
Fuente Sierra 4	2 (29%)	5 (71%)		7
La Retama	49 (59%)	34 (41%)		83
La Col-D	28 (53%)	25 (47%)		53
La Col-C	21 (30%)	47 (67%)	2 (3%)	70
La Col-B	2 (25%)	6 (75%)		8
Valtorres (type material+MNCN)	19 (39%)	30 (61%)		49
Valtorres type Material	10 (40%)	15 (60%)		25
Valtorres extra type Material	1 (9%)	10 (91%)		11
Valtorres MNCN	8 (62%)	5 (38%)		13
Fuente Sierra 3	4 (67%)	2 (33%)		6
Fuente Sierra 2	4 (67%)	2 (33%)		6
Vargas 2B	5 (56%)	4 (44%)		9
Olmo Redondo 9	17 (61%)	11 (39%)		28
La Col-A		5 (100%)		5
Vargas 2A	2 (50%)	2 (50%)		4
Olmo Redondo 8	12 (50%)	12 (50%)		24
Olmo Redondo 5	6 (46%)	7 (54%)		13
Vargas 3	4 (24%)	13 (76%)		17
Vargas 1A	22 (42%)	31 (58%)		53
Vargas 4BB	7 (27%)	19 (73%)		26
Vargas 4B	1 (25%)	3 (75%)		4
Vargas 4A	6 (17%)	29 (83%)		35
Olmo Redondo 4A	4 (36%)	7 (64%)		11
San Roque 3		4 (100%)		4
Artesilla	25 (22%)	87 (77%)	1 (1%)	113

Table 4. Labial Spur of the Anterolophule M1

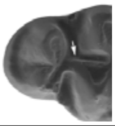
Localities				N
Valdemoros 1A	5 (18%)	2 (7%)	21 (75%)	28
Valdemoros 8A	3 (21%)	1 (7%)	10 (71%)	14
Moratilla 3	1 (33%)	1 (33%)	1 (33%)	3
Moratilla 2	1 (17%)		5 (83%)	6
Fuente Sierra 4	1 (14%)	1 (14%)	5 (71%)	7
La Retama	22 (23%)	4 (4%)	71 (73%)	97
La Col-D	16 (26%)	7 (11%)	39 (63%)	62
La Col-C	16 (21%)	7 (9%)	52 (69%)	75
La Col-B	2 (20%)		8 (80%)	10
Valtorres (type material+MNCN)	10 (19%)	2 (4%)	41 (77%)	53
Valtorres type Material	1 (4%)		24 (96%)	25
Valtorres extra type Material	7 (47%)	1 (7%)	7 (47%)	15
Valtorres MNCN	2 (15%)	1 (8%)	10 (77%)	13
Fuente Sierra 3	1 (13%)	1 (13%)	6 (75%)	8
Fuente Sierra 2	2 (33%)		4 (67%)	6
Vargas 2B	2 (20%)	1 (10%)	7 (70%)	10
Olmo Redondo 9	8 (29%)	3 (11%)	17 (61%)	28
La Col-A	1 (14%)		6 (86%)	7
Vargas 2A	1 (17%)	1 (17%)	4 (67%)	6
Olmo Redondo 8	10 (34%)	2 (7%)	17 (59%)	29
Olmo Redondo 5	5 (36%)	1 (7%)	8 (57%)	14
Vargas 3	6 (26%)	1 (4%)	16 (70%)	23
Vargas 1A	16 (24%)	6 (9%)	44 (67%)	66
Vargas 4BB	10 (31%)		22 (69%)	32
Vargas 4B			4 (100%)	4
Vargas 4A	3 (7%)	3 (7%)	35 (85%)	41
Olmo Redondo 4A	5 (42%)	1 (8%)	6 (50%)	12
San Roque 3	1 (25%)		3 (75%)	4
Artesilla	23 (19%)	8 (7%)	88 (74%)	119

Table 5. Protolophule of the M1

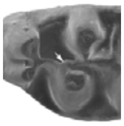
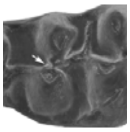
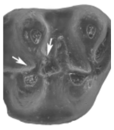
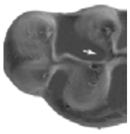
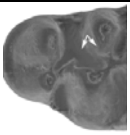
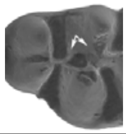
Localities							N
Valdemoros 1A				24 (86%)	2 (7%)	2 (7%)	28
Valdemoros 8A				10 (77%)	2 (15%)	1 (8%)	13
Moratilla 3					1 (50%)	1 (50%)	2
Moratilla 2				6 (100%)			6
Fuente Sierra 4				6 (100%)			6
La Retama			1 (1%)	69 (79%)	11 (13%)	6 (7%)	87
La Col-D				37 (71%)	9 (17%)	6 (12%)	52
La Col-C	1 (1%)			63 (86%)	6 (8%)	3 (4%)	73
La Col-B				9 (100%)			9
Valtorres (type material+MNCN)				35 (80%)	7 (16%)	2 (5%)	44
Valtorres type Material				15 (79%)	3 (16%)	1 (5%)	19
Valtorres extra type Material				7 (64%)	3 (27%)	1 (9%)	11
Valtorres MNCN				13 (93%)	1 (7%)		14
Fuente Sierra 3				5 (71%)	2 (29%)		7
Fuente Sierra 2				3 (50%)	3 (50%)		6
Vargas 2B				7 (78%)	1 (11%)	1 (11%)	9
Olmo Redondo 9				26 (84%)	4 (13%)	1 (3%)	31
La Col-A				7 (100%)			7
Vargas 2A				4 (67%)	2 (33%)		6
Olmo Redondo 8				21 (78%)	4 (15%)	2 (7%)	27
Olmo Redondo 5	1 (7%)			12 (80%)	1 (7%)	1 (7%)	15
Vargas 3				17 (74%)	3 (13%)	3 (13%)	23
Vargas 1A				55 (85%)	5 (8%)	5 (8%)	65
Vargas 4BB				19 (68%)	7 (25%)	2 (7%)	28
Vargas 4B				4 (100%)			4
Vargas 4A				34 (87%)	3 (8%)	2 (5%)	39
Olmo Redondo 4A				9 (90%)		1 (10%)	10
San Roque 3				4 (100%)			4
Artesilla		2 (2%)		85 (88%)	8 (8%)	2 (2%)	97

Table 6. Ectoloph M1

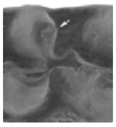
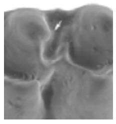
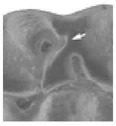
Localities				N
Valdemoros 1A	2 (7%)	19 (68%)	7 (25%)	28
Valdemoros 8A	8 (62%)	5 (38%)		13
Moratilla 3	1 (100%)			1
Moratilla 2	3 (60%)	2 (40%)		5
Fuente Sierra 4	3 (43%)	3 (43%)	1 (14%)	7
La Retama	60 (63%)	34 (36%)	1 (1%)	95
La Col-D	33 (59%)	21 (38%)	2 (4%)	56
La Col-C	17 (26%)	45 (68%)	4 (6%)	66
La Col-B	3 (33%)	4 (44%)	2 (22%)	9
Valtorres (type material+MNCN)	20 (38%)	27 (51%)	6 (11%)	53
Valtorres type Material	7 (29%)	13 (54%)	4 (17%)	24
Valtorres extra type Material	7 (50%)	6 (43%)	1 (7%)	14
Valtorres MNCN	6 (40%)	8 (53%)	1 (7%)	15
Fuente Sierra 3	5 (71%)	2 (29%)		7
Fuente Sierra 2	1 (17%)	4 (67%)	1 (17%)	6
Vargas 2B	2 (18%)	8 (73%)	1 (9%)	11
Olmo Redondo 9	10 (34%)	18 (62%)	1 (3%)	29
La Col-A	4 (50%)	4 (50%)		8
Vargas 2A	2 (33%)	4 (67%)		6
Olmo Redondo 8	6 (23%)	20 (77%)		26
Olmo Redondo 5	6 (43%)	8 (57%)		14
Vargas 3	7 (29%)	16 (67%)	1 (4%)	24
Vargas 1A	15 (23%)	48 (74%)	2 (3%)	65
Vargas 4BB	14 (42%)	18 (55%)	1 (3%)	33
Vargas 4B	2 (40%)	2 (40%)	1 (20%)	5
Vargas 4A	13 (32%)	28 (68%)		41
Olmo Redondo 4A	1 (8%)	11 (85%)	1 (8%)	13
San Roque 3		3 (75%)	1 (25%)	4
Artesilla	13 (11%)	70 (57%)	39 (32%)	122

Table 7. Mesoloph M1

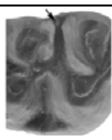
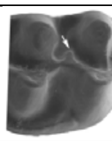
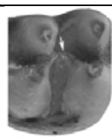
Localities					N
Valdemoros 1A		10 (37%)	16 (59%)	1 (4%)	27
Valdemoros 8A		2 (15%)	11 (85%)		13
Moratilla 3		1 (50%)	1 (50%)		2
Moratilla 2			4 (80%)	1 (20%)	5
Fuente Sierra 4		3 (38%)	5 (63%)		8
La Retama	1 (1%)	26 (26%)	67 (66%)	7 (7%)	101
La Col-D	3 (4%)	21 (31%)	42 (62%)	2 (3%)	68
La Col-C		33 (46%)	36 (51%)	2 (3%)	71
La Col-B		6 (67%)	2 (22%)	1 (11%)	9
Valtorres (type material+MNCN)	1 (2%)	20 (40%)	25 (50%)	4 (8%)	50
Valtorres type Material	1 (4%)	9 (38%)	11 (46%)	3 (13%)	24
Valtorres extra type Material		7 (54%)	6 (46%)		13
Valtorres MNCN		4 (31%)	8 (62%)	1 (8%)	13
Fuente Sierra 3		2 (22%)	7 (78%)		9
Fuente Sierra 2		2 (40%)	3 (60%)		5
Vargas 2B		5 (50%)	5 (50%)		10
Olmo Redondo 9		11 (34%)	21 (66%)		32
La Col-A		2 (29%)	5 (71%)		7
Vargas 2A		5 (63%)	2 (25%)	1 (13%)	8
Olmo Redondo 8	2 (6%)	11 (35%)	17 (55%)	1 (3%)	31
Olmo Redondo 5		8 (57%)	5 (36%)	1 (7%)	14
Vargas 3	1 (5%)	10 (48%)	8 (38%)	2 (10%)	21
Vargas 1A	2 (3%)	28 (42%)	35 (53%)	1 (2%)	66
Vargas 4BB	2 (6%)	14 (42%)	17 (52%)		33
Vargas 4B		3 (60%)	2 (40%)		5
Vargas 4A	5 (12%)	15 (36%)	21 (50%)	1 (2%)	42
Olmo Redondo 4A		9 (82%)	2 (18%)		11
San Roque 3		3 (75%)	1 (25%)		4
Artesilla	9 (7%)	79 (65%)	33 (27%)		121

Table 8. Lingual mesocingulum of the M1.

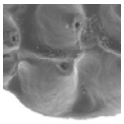
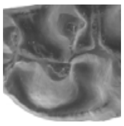
Localities			N
Valdemoros 1A	17 (65%)	9 (35%)	26
Valdemoros 8A	4 (29%)	10 (71%)	14
Moratilla 3		3 (100%)	3
Moratilla 2		5 (100%)	5
Fuente Sierra 4	4 (80%)	1 (20%)	5
La Retama	41 (42%)	57 (58%)	98
La Col-D	26 (39%)	40 (61%)	66
La Col-C	41 (58%)	30 (42%)	71
La Col-B	4 (44%)	5 (56%)	9
Valtorres (type material+MNCN)	34 (63%)	20 (37%)	54
Valtorres type Material	16 (64%)	9 (36%)	25
Valtorres extra type Material	9 (60%)	6 (40%)	15
Valtorres MNCN	9 (64%)	5 (36%)	14
Fuente Sierra 3	3 (38%)	5 (63%)	8
Fuente Sierra 2	2 (33%)	4 (67%)	6
Vargas 2B	4 (44%)	5 (56%)	9
Olmo Redondo 9	12 (41%)	17 (59%)	29
La Col-A	7 (88%)	1 (13%)	8
Vargas 2A	3 (50%)	3 (50%)	6
Olmo Redondo 8	14 (52%)	13 (48%)	27
Olmo Redondo 5	5 (33%)	10 (67%)	15
Vargas 3	17 (71%)	7 (29%)	24
Vargas 1A	46 (69%)	21 (31%)	67
Vargas 4BB	21 (70%)	9 (30%)	30
Vargas 4B	5 (100%)		5
Vargas 4A	24 (62%)	15 (38%)	39
Olmo Redondo 4A	11 (100%)		11
San Roque 3	3 (100%)		3
Artesilla	102 (84%)	19 (16%)	121

Table 9. Connection Mesoloph-Ectoloph M1

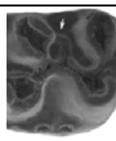
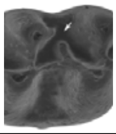
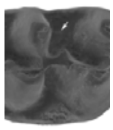
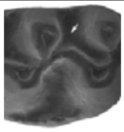
Localities					N
Valdemoros 1A	3 (11%)	21 (78%)	2 (7%)	1 (4%)	27
Valdemoros 8A	1 (8%)	4 (31%)	8 (62%)		13
Moratilla 3			1 (100%)		1
Moratilla 2		2 (40%)	3 (60%)		5
Fuente Sierra 4		4 (57%)	3 (43%)		7
La Retama	3 (3%)	30 (33%)	54 (59%)	4 (4%)	91
La Col-D	1 (2%)	22 (40%)	31 (56%)	1 (2%)	55
La Col-C	3 (5%)	41 (67%)	15 (25%)	2 (3%)	61
La Col-B		5 (56%)	3 (33%)	1 (11%)	9
Valtorres (type material+MNCN)	1 (2%)	26 (52%)	18 (36%)	5 (10%)	50
Valtorres type Material	1 (4%)	12 (50%)	7 (29%)	4 (17%)	24
Valtorres extra type Material		6 (46%)	7 (54%)		13
Valtorres MNCN		8 (62%)	4 (31%)	1 (8%)	13
Fuente Sierra 3		2 (29%)	5 (71%)		7
Fuente Sierra 2	1 (20%)	3 (60%)	1 (20%)		5
Vargas 2B		9 (82%)	2 (18%)		11
Olmo Redondo 9		21 (75%)	7 (25%)		28
La Col-A		1 (17%)	5 (83%)		6
Vargas 2A		4 (67%)	2 (33%)		6
Olmo Redondo 8		21 (81%)	4 (15%)	1 (4%)	26
Olmo Redondo 5		8 (62%)	4 (31%)	1 (8%)	13
Vargas 3		15 (68%)	5 (23%)	2 (9%)	22
Vargas 1A	1 (2%)	46 (74%)	14 (23%)	1 (2%)	62
Vargas 4BB		20 (61%)	13 (39%)		33
Vargas 4B		3 (75%)	1 (25%)		4
Vargas 4A		28 (70%)	11 (28%)	1 (3%)	40
Olmo Redondo 4A		10 (91%)	1 (9%)		11
San Roque 3		4 (100%)			4
Artesilla	5 (5%)	87 (81%)	16 (15%)		108

Table 10. Metalophule M1

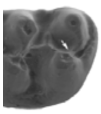
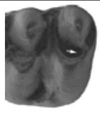
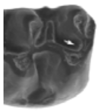
Localities									N
Valdemoros 1A				3 (13%)	19 (79%)	2 (8%)			24
Valdemoros 8A					12 (92%)	1 (8%)			13
Moratilla 3				1 (100%)					1
Moratilla 2				2 (33%)	4 (67%)				6
Fuente Sierra 4					7 (100%)				7
La Retama	1 (1%)	4 (5%)	4 (5%)	9 (12%)	56 (76%)				74
La Col-D		4 (7%)	3 (5%)	3 (5%)	40 (73%)	2 (4%)		3 (5%)	55
La Col-C		2 (3%)	3 (5%)	6 (9%)	54 (83%)				65
La Col-B		1 (14%)		2 (29%)	4 (57%)				7
Valtorres (type material+MNCN)				6 (13%)	38 (84%)	1 (2%)			45
Valtorres type Material				3 (14%)	18 (86%)				21
Valtorres extra type Material				1 (9%)	9 (82%)	1 (9%)			11
Valtorres MNCN				2 (15%)	11 (85%)				13
Fuente Sierra 3					5 (71%)	2 (29%)			7
Fuente Sierra 2				2 (29%)	5 (71%)				7
Vargas 2B		1 (11%)	1 (11%)	1 (11%)	5 (56%)	1 (11%)			9
Olmo Redondo 9		1 (4%)	4 (15%)	4 (15%)	17 (63%)	1 (4%)			27
La Col-A		1 (50%)			1 (50%)				2
Vargas 2A			1 (17%)		5 (83%)				6
Olmo Redondo 8				1 (4%)	25 (93%)	1 (4%)			27
Olmo Redondo 5				3 (23%)	10 (77%)				13
Vargas 3		1 (5%)	3 (14%)	3 (14%)	13 (62%)			1 (5%)	21
Vargas 1A		1 (2%)	2 (3%)	11 (18%)	48 (77%)				62
Vargas 4BB		1 (4%)		4 (15%)	20 (74%)		2 (7%)		27
Vargas 4B				1 (25%)	3 (75%)				4
Vargas 4A			1 (3%)	4 (11%)	32 (84%)			1 (3%)	38
Olmo Redondo 4A				2 (20%)	8 (80%)				10
San Roque 3					3 (100%)				3
Artesilla	1 (1%)	1 (1%)	1 (1%)	17 (16%)	85 (80%)		1 (1%)		106

Table 11. Protolophule M2

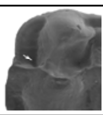
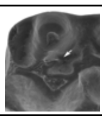
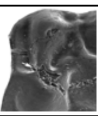
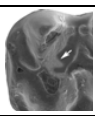
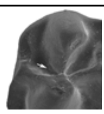
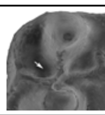
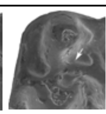
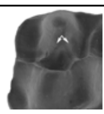
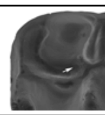
Localities										N
Valdemoros 1A	6 (46%)					1 (8%)	1 (8%)	5 (38%)		13
Valdemoros 8A	2 (40%)	1 (20%)	2 (40%)							5
Moratilla 2	2 (100%)									2
Fuente Sierra 4	8 (62%)	2 (15%)	3 (23%)							13
La Retama	61 (78%)	11 (14%)	4 (5%)		1 (1%)			1 (1%)		78
La Col-D	41 (64%)	14 (22%)	5 (8%)					3 (5%)	1 (2%)	64
La Col-C	22 (49%)	13 (29%)	6 (13%)		1 (2%)			3 (7%)		45
La Col-B	3 (60%)	1 (20%)						1 (20%)		5
Valtorres (type material+MNCN)	25 (50%)	12 (24%)	6 (12%)	1 (2%)		1 (2%)		5 (10%)		50
Valtorres type Material	8 (31%)	6 (23%)	5 (19%)	1 (4%)		1 (4%)		5 (19%)		26
Valtorres extra type Material	2 (33%)	3 (50%)	1 (17%)							6
Valtorres MNCN	15 (83%)	3 (17%)								18
Fuente Sierra 3	4 (67%)	1 (17%)	1 (17%)							6
Fuente Sierra 2	4 (44%)	3 (33%)						2 (22%)		9
Vargas 2B	4 (40%)	5 (50%)	1 (10%)							10
Olmo Redondo 9	15 (68%)	5 (23%)						1 (5%)	1 (5%)	22
La Col-A	2 (25%)	3 (38%)	1 (13%)					2 (25%)		8
Vargas 2A	7 (44%)	6 (38%)	2 (13%)					1 (6%)		16
Olmo Redondo 8	18 (62%)	7 (24%)	1 (3%)			1 (3%)		2 (7%)		29
Olmo Redondo 5	4 (36%)	4 (36%)						3 (27%)		11
Vargas 3	13 (62%)	6 (29%)						2 (10%)		21
Vargas 1A	52 (79%)	9 (14%)	2 (3%)					3 (5%)		66
Vargas 4BB	13 (43%)	8 (27%)	2 (7%)		1 (3%)			6 (20%)		30
Vargas 4B	1 (25%)	2 (50%)				1 (25%)				4
Vargas 4A	19 (54%)	8 (23%)	7 (20%)					1 (3%)		35
Olmo Redondo 4A	8 (67%)	2 (17%)			1 (8%)			1 (8%)		12
San Roque 3	1 (33%)	1 (33%)	1 (33%)							3
Artesilla	63 (61%)	28 (27%)	7 (7%)		1 (1%)			5 (5%)		104

Table 12. Anterior Protolophule M2

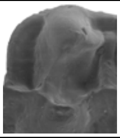
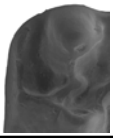
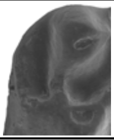
Localities				N
Valdemoros 1A	6 (100%)			6
Valdemoros 8A	2 (67%)		1 (33%)	3
Moratilla 2		2 (100%)		2
Fuente Sierra 4	8 (80%)	2 (20%)		10
La Retama	67 (93%)	4 (6%)	1 (1%)	72
La Col-D	53 (96%)	2 (4%)		55
La Col-C	35 (100%)			35
La Col-B	4 (100%)			4
Valtorres (type material+MNCN)	35 (95%)	2 (5%)		37
Valtorres type Material	14 (100%)			14
Valtorres extra UU Material	5 (100%)			5
Valtorres MNCN	16 (89%)	2 (11%)		18
Fuente Sierra 3	5 (100%)			5
Fuente Sierra 2	12 (100%)			12
Vargas 2B	9 (100%)			9
La Col-A	5 (100%)			5
Vargas 2A	13 (100%)			13
Vargas 3	19 (100%)			19
Vargas 4BB	21 (100%)			21
Vargas 4B	3 (100%)			3
Vargas 4A	27 (100%)			27
San Roque 3	2 (100%)			2
Artesilla	91 (100%)			91

Table 13. Ectoloph M2

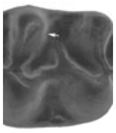
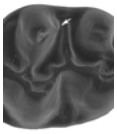
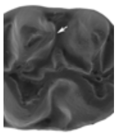
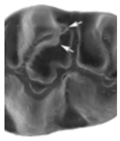
Localities					N
Valdemoros 1A		8 (47%)	9 (53%)		17
Valdemoros 8A	2 (29%)	4 (57%)	1 (14%)		7
Moratilla 2		1 (100%)			1
Fuente Sierra 4	4 (33%)	4 (33%)	4 (33%)		12
La Retama	11 (12%)	48 (51%)	35 (37%)		94
La Col-D	8 (14%)	24 (41%)	26 (45%)		58
La Col-C	8 (17%)	21 (44%)	19 (40%)		48
La Col-B		3 (43%)	4 (57%)		7
Valtorres (type material+MNCN)	10 (22%)	19 (42%)	16 (36%)		45
Valtorres type Material	3 (13%)	9 (39%)	11 (48%)		23
Valtorres extra type Material	1 (20%)	2 (40%)	2 (40%)		5
Valtorres MNCN	6 (35%)	8 (47%)	3 (18%)		17
Fuente Sierra 3	3 (30%)	4 (40%)	3 (30%)		10
Fuente Sierra 2	3 (30%)	2 (20%)	4 (40%)	1 (10%)	10
Vargas 2B	4 (40%)	3 (30%)	3 (30%)		10
Olmo Redondo 9	6 (29%)	6 (29%)	9 (43%)		21
La Col-A	4 (40%)	5 (50%)	1 (10%)		10
Vargas 2A	3 (23%)	8 (62%)	2 (15%)		13
Olmo Redondo 8	2 (6%)	22 (69%)	8 (25%)		32
Olmo Redondo 5	4 (29%)	5 (36%)	4 (29%)	1 (7%)	14
Vargas 3	1 (5%)	11 (50%)	10 (45%)		22
Vargas 1A	4 (6%)	40 (59%)	23 (34%)	1 (1%)	68
Vargas 4BB	8 (25%)	13 (41%)	11 (34%)		32
Vargas 4B	1 (17%)	3 (50%)	2 (33%)		6
Vargas 4A	2 (6%)	26 (72%)	8 (22%)		36
Olmo Redondo 4A		7 (54%)	6 (46%)		13
San Roque 3		1 (33%)	2 (67%)		3
Artesilla	6 (6%)	45 (42%)	57 (53%)	1 (1%)	109

Table 14. Mesoloph M2

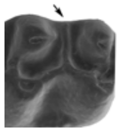
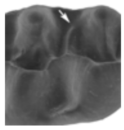
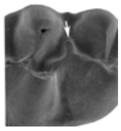
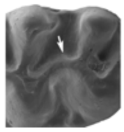
Localities					N
Valdemoros 1A	1 (6%)	7 (44%)	8 (50%)		16
Valdemoros 8A	2 (33%)	3 (50%)	1 (17%)		6
Moratilla 2	1 (50%)	1 (50%)			2
Fuente Sierra 4	2 (17%)	5 (42%)	5 (42%)		12
La Retama	12 (13%)	36 (38%)	46 (49%)		94
La Col-D	11 (17%)	35 (55%)	18 (28%)		64
La Col-C	12 (23%)	26 (50%)	14 (27%)		52
La Col-B	2 (29%)	5 (71%)			7
Valtorres (type material+MNCN)	8 (16%)	27 (55%)	12 (24%)	2 (4%)	49
Valtorres type Material	3 (12%)	17 (68%)	5 (20%)		25
Valtorres extra type Material	1 (14%)	4 (57%)	2 (29%)		7
Valtorres MNCN	4 (22%)	7 (39%)	5 (28%)	2 (11%)	18
Fuente Sierra 3	5 (56%)	3 (33%)		1 (11%)	9
Fuente Sierra 2	2 (18%)	6 (55%)	3 (27%)		11
Vargas 2B		7 (78%)	2 (22%)		9
Olmo Redondo 9	3 (16%)	7 (37%)	9 (47%)		19
La Col-A	1 (13%)	1 (13%)	6 (75%)		8
Vargas 2A		10 (63%)	6 (38%)		16
Olmo Redondo 8	4 (13%)	17 (57%)	9 (30%)		30
Olmo Redondo 5	2 (14%)	8 (57%)	4 (29%)		14
Vargas 3	4 (18%)	9 (41%)	9 (41%)		22
Vargas 1A	10 (14%)	31 (44%)	30 (42%)		71
Vargas 4BB	5 (15%)	16 (47%)	12 (35%)	1 (3%)	34
Vargas 4B		7 (100%)			7
Vargas 4A	13 (37%)	11 (31%)	11 (31%)		35
Olmo Redondo 4A	1 (7%)	9 (64%)	4 (29%)		14
San Roque 3		3 (100%)			3
Artesilla	11 (10%)	56 (51%)	38 (35%)	4 (4%)	109

Table 15. Connection Mesolph-Ectoloph M2

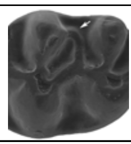
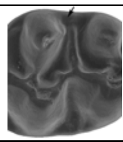
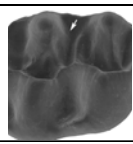
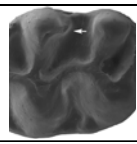
Localities					N
Valdemoros 1A	3 (19%)	13 (81%)			16
Valdemoros 8A	1 (17%)	3 (50%)	2 (33%)		6
Moratilla 2	1 (100%)				1
Fuente Sierra 4	2 (17%)	6 (50%)	4 (33%)		12
La Retama	34 (37%)	48 (52%)	10 (11%)		92
La Col-D	13 (24%)	35 (64%)	7 (13%)		55
La Col-C	12 (26%)	25 (54%)	8 (17%)	1 (2%)	46
La Col-B	3 (43%)	4 (57%)			7
Valtorres (type material+MNCN)	7 (15%)	29 (60%)	10 (21%)	2 (4%)	48
Valtorres type Material	5 (21%)	16 (67%)	2 (8%)	1 (4%)	24
Valtorres extra type Material		5 (83%)	1 (17%)		6
Valtorres MNCN	2 (11%)	8 (44%)	7 (39%)	1 (6%)	18
Fuente Sierra 3	1 (14%)	3 (43%)	3 (43%)		7
Fuente Sierra 2	3 (30%)	4 (40%)	3 (30%)		10
Vargas 2B	2 (25%)	3 (38%)	3 (38%)		8
Olmo Redondo 9	6 (30%)	14 (70%)			20
La Col-A		5 (63%)	3 (38%)		8
Vargas 2A	1 (8%)	8 (67%)	3 (25%)		12
Olmo Redondo 8	7 (22%)	24 (75%)	1 (3%)		32
Olmo Redondo 5	3 (21%)	7 (50%)	4 (29%)		14
Vargas 3	4 (18%)	17 (77%)	1 (5%)		22
Vargas 1A	15 (22%)	49 (72%)	4 (6%)		68
Vargas 4BB	1 (4%)	21 (75%)	6 (21%)		28
Vargas 4B	3 (50%)	2 (33%)	1 (17%)		6
Vargas 4A	5 (15%)	27 (79%)	2 (6%)		34
Olmo Redondo 4A	5 (38%)	8 (62%)			13
San Roque 3		3 (100%)			3
Artesilla	12 (13%)	71 (74%)	8 (8%)	5 (5%)	96

Table 16. Metalophule M2

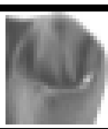
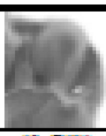
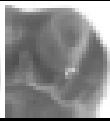
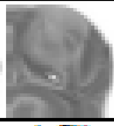
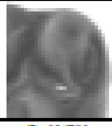
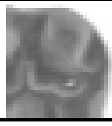
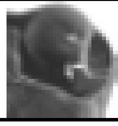
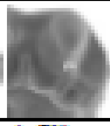
Localities									N
Valdemoros 1A		10 (71%)		1 (7%)	2 (14%)			1 (7%)	14
Valdemoros 8A		4 (80%)			1 (20%)				5
Moratilla 2		1 (100%)							1
Fuente Sierra 4		10 (83%)		2 (17%)					12
La Retama	1 (1%)	56 (79%)		5 (7%)	7 (10%)	2 (3%)			71
La Col-D	1 (2%)	46 (74%)	1 (2%)	7 (11%)	5 (8%)		2 (3%)		62
La Col-C		36 (80%)		2 (4%)	2 (4%)	2 (4%)		3 (7%)	45
La Col-B		5 (83%)			1 (17%)				6
Valtorres (type material+MNCN)		25 (56%)		7 (16%)	9 (20%)	3 (7%)		1 (2%)	45
Valtorres type Material		10 (43%)		4 (17%)	6 (26%)	2 (9%)		1 (4%)	23
Valtorres extra type Material		3 (75%)			1 (25%)				4
Valtorres MNCN		12 (67%)		3 (17%)	2 (11%)	1 (6%)			18
Fuente Sierra 3		2 (33%)		2 (33%)	2 (33%)				6
Fuente Sierra 2		6 (60%)				3 (30%)		1 (10%)	10
Vargas 2B		8 (89%)			1 (11%)				9
Olmo Redondo 9		17 (81%)	1 (5%)		1 (5%)	2 (10%)			21
La Col-A		5 (63%)		1 (13%)		1 (13%)		1 (13%)	8
Vargas 2A	1 (7%)	8 (53%)		3 (20%)	2 (13%)			1 (7%)	15
Olmo Redondo 8		20 (71%)	2 (7%)	1 (4%)	3 (11%)	2 (7%)			28
Olmo Redondo 5		6 (60%)			3 (30%)			1 (10%)	10
Vargas 3		14 (61%)	2 (9%)	5 (22%)	2 (9%)				23
Vargas 1A	1 (2%)	43 (65%)		3 (5%)	14 (21%)	1 (2%)	2 (3%)	2 (3%)	66
Vargas 4BB		17 (59%)	1 (3%)	2 (7%)	7 (24%)			2 (7%)	29
Vargas 4B		3 (75%)			1 (25%)				4
Vargas 4A		15 (43%)		9 (26%)	8 (23%)	1 (3%)		2 (6%)	35
Olmo Redondo 4A		12 (100%)							12
San Roque 3				1 (33%)	2 (67%)				3
Artesilla		64 (64%)		25 (25%)	11 (11%)				100

Table 17. Metalophule M3

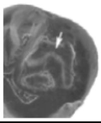
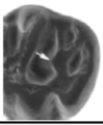
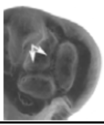
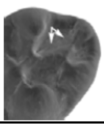
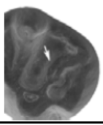
Localities								N
Valdemoros 1A		1 (17%)	2 (33%)	1 (17%)	2 (33%)			6
La Retama	1 (33%)	1 (33%)			1 (33%)			3
La Col-C					1 (50%)		1 (50%)	2
Valtorres (type material+MNCN)	1 (6%)	3 (17%)	8 (44%)	1 (6%)	3 (17%)	2 (11%)		18
Valtorres type Material	1 (6%)	3 (18%)	7 (41%)	1 (6%)	3 (18%)	2 (12%)		17
Valtorres extra type Material			1 (100%)					1
Olmo Redondo 8		2 (100%)						2
Olmo Redondo 5					1 (100%)			1
Vargas 1A		1 (33%)	2 (67%)					3
Olmo Redondo 4A		1 (50%)					1 (50%)	2
San Roque 3			3 (100%)					3
Artesilla		3 (30%)	6 (60%)			1 (10%)		10

Table 18. Anteroconid m1

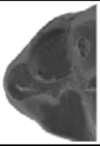
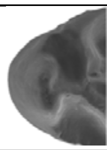
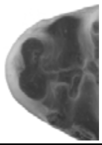
Localities				N
Valdemoros 1A	26 (96%)	1 (4%)		27
Valdemoros 8A	3 (100%)			3
Fuente Sierra 4	7 (100%)			7
La Retama	50 (94%)	3 (6%)		53
La Col-D	23 (96%)		1 (4%)	24
La Col-C	47 (96%)	1 (2%)	1 (2%)	49
La Col-B	3 (100%)			3
Valtorres (type material+MNCN)	43 (100%)			43
Valtorres type Material	28 (100%)			28
Valtorres extra type Material	4 (100%)			4
Valtorres MNCN	11 (100%)			11
Fuente Sierra 3	6 (100%)			6
Fuente Sierra 2	11 (100%)			11
Vargas 2B	9 (100%)			9
Olmo Redondo 9	8 (100%)			8
La Col-A	7 (88%)	1 (13%)		8
Vargas 2A	4 (100%)			4
Olmo Redondo 8	22 (100%)			22
Olmo Redondo 5	7 (78%)	2 (22%)		9
Vargas 3	15 (88%)	2 (12%)		17
Vargas 1A	48 (94%)	2 (4%)	1 (2%)	51
Vargas 4BB	17 (100%)			17
Vargas 4B	7 (100%)			7
Vargas 4A	27 (93%)	2 (7%)		29
Olmo Redondo 4A	5 (100%)			5
San Roque 3	2 (100%)			2
Artesilla	120 (98%)	2 (2%)		122

Table 19. Labial Spur of the Anterolophulid m1

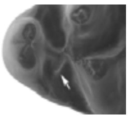
Localities				N
Valdemoros 1A	25 (93%)	2 (7%)		27
Valdemoros 8A	3 (100%)			3
Fuente Sierra 4	6 (75%)	1 (13%)	1 (13%)	8
La Retama	67 (92%)	2 (3%)	4 (5%)	73
La Col-D	33 (85%)		6 (15%)	39
La Col-C	52 (90%)	1 (2%)	5 (9%)	58
La Col-B	3 (100%)			3
Valtorres (type material+MNCN)	45 (94%)		3 (6%)	48
Valtorres type Material	29 (97%)		1 (3%)	30
Valtorres extra type Material	5 (83%)		1 (17%)	6
Valtorres MNCN	11 (92%)		1 (8%)	12
Fuente Sierra 3	6 (100%)			6
Fuente Sierra 2	10 (83%)		2 (17%)	12
Vargas 2B	10 (100%)			10
Olmo Redondo 9	2 (18%)	1 (9%)	8 (73%)	11
La Col-A	10 (100%)			10
Vargas 2A	3 (75%)		1 (25%)	4
Olmo Redondo 8	20 (83%)		4 (17%)	24
Olmo Redondo 5	13 (93%)		1 (7%)	14
Vargas 3	17 (85%)		3 (15%)	20
Vargas 1A	47 (76%)	1 (2%)	14 (23%)	62
Vargas 4BB	16 (94%)		1 (6%)	17
Vargas 4B	3 (43%)	1 (14%)	3 (43%)	7
Vargas 4A	29 (94%)		2 (6%)	31
Olmo Redondo 4A	1 (25%)		3 (75%)	4
San Roque 3	2 (100%)			2
Artesilla	107 (90%)	5 (4%)	7 (6%)	119

Table 20. Metalophulid m1

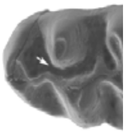
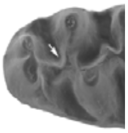
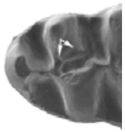
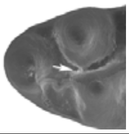
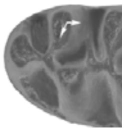
Localities						N
Valdemoros 1A		23 (88%)	3 (12%)			26
Valdemoros 8A		1 (50%)	1 (50%)			2
Fuente Sierra 4		6 (75%)			2 (25%)	8
La Retama	1 (1%)	57 (84%)	6 (9%)		4 (6%)	68
La Col-D	1 (2%)	28 (74%)	6 (16%)		3 (8%)	38
La Col-C		46 (73%)	12 (19%)	1 (2%)	4 (6%)	63
La Col-B		1 (50%)	1 (50%)			2
Valtorres (type material+MNCN)		42 (82%)	7 (14%)		2 (4%)	51
Valtorres type Material		24 (77%)	6 (19%)		1 (3%)	31
Valtorres extra type Material		6 (86%)	1 (14%)			7
Valtorres MNCN		12 (92%)			1 (8%)	13
Fuente Sierra 3		5 (83%)			1 (17%)	6
Fuente Sierra 2		10 (77%)	2 (15%)		1 (8%)	13
Vargas 2B		7 (70%)	1 (10%)		2 (20%)	10
Olmo Redondo 9		11 (85%)	1 (8%)		1 (8%)	13
La Col-A		7 (64%)	3 (27%)		1 (9%)	11
Vargas 2A		6 (100%)				6
Olmo Redondo 8		22 (88%)	2 (8%)		1 (4%)	25
Olmo Redondo 5		14 (88%)	1 (6%)		1 (6%)	16
Vargas 3		19 (90%)	1 (5%)		1 (5%)	21
Vargas 1A		65 (96%)			3 (4%)	68
Vargas 4BB		21 (84%)	3 (12%)		1 (4%)	25
Vargas 4B		7 (100%)				7
Vargas 4A		37 (95%)	1 (3%)		1 (3%)	39
Olmo Redondo 4A		4 (100%)				4
San Roque 3		2 (100%)				2
Artesilla	1 (1%)	125 (93%)	7 (5%)		1 (1%)	134

Table 21. Mesolophid m1

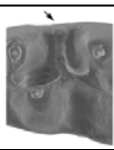
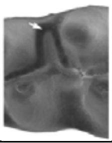
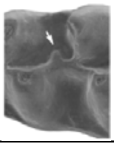
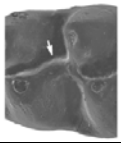
Localities					N
Valdemoros 1A			20 (77%)	6 (23%)	26
Valdemoros 8A			3 (100%)		3
Fuente Sierra 4			8 (100%)		8
La Retama		8 (11%)	56 (80%)	6 (9%)	70
La Col-D	3 (7%)	5 (12%)	32 (74%)	3 (7%)	43
La Col-C	2 (3%)	11 (18%)	42 (70%)	5 (8%)	60
La Col-B	1 (33%)		2 (67%)		3
Valtorres (type material+MNCN)		6 (12%)	41 (82%)	3 (6%)	50
Valtorres type Material		3 (10%)	24 (80%)	3 (10%)	30
Valtorres extra type Material		1 (14%)	6 (86%)		7
Valtorres MNCN		2 (15%)	11 (85%)		13
Fuente Sierra 3	1 (20%)		4 (80%)		5
Fuente Sierra 2	1 (7%)	3 (21%)	8 (57%)	2 (14%)	14
Vargas 2B	1 (11%)	3 (33%)	5 (56%)		9
Olmo Redondo 9		1 (6%)	15 (88%)	1 (6%)	17
La Col-A		2 (17%)	10 (83%)		12
Vargas 2A	1 (17%)	1 (17%)	2 (33%)	2 (33%)	6
Olmo Redondo 8	1 (4%)	6 (23%)	19 (73%)		26
Olmo Redondo 5		4 (22%)	14 (78%)		18
Vargas 3		5 (24%)	15 (71%)	1 (5%)	21
Vargas 1A		11 (16%)	55 (80%)	3 (4%)	69
Vargas 4BB		6 (25%)	16 (67%)	2 (8%)	24
Vargas 4B		4 (57%)	2 (29%)	1 (14%)	7
Vargas 4A	1 (3%)	7 (19%)	28 (78%)		36
Olmo Redondo 4A		1 (13%)	7 (88%)		8
San Roque 3			2 (100%)		2
Artesilla	2 (2%)	47 (36%)	78 (59%)	5 (4%)	132

Table 22. Ectomesolophid m1

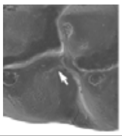
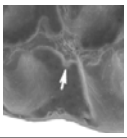
Localities				N
Valdemoros 1A	26 (100%)			26
Valdemoros 8A	4 (100%)			4
Fuente Sierra 4	8 (100%)			8
La Retama	77 (100%)			77
La Col-D	43 (96%)		2 (4%)	45
La Col-C	60 (92%)	3 (5%)	2 (3%)	65
La Col-B	3 (100%)			3
Valtorres (type material+MNCN)	51 (96%)		2 (4%)	53
Valtorres type Material	31 (97%)		1 (3%)	32
Valtorres extra type Material	7 (88%)		1 (13%)	8
Valtorres MNCN	13 (100%)			13
Fuente Sierra 3	5 (100%)			5
Fuente Sierra 2	13 (100%)			13
Vargas 2B	10 (83%)		2 (17%)	12
Olmo Redondo 9	17 (94%)		1 (6%)	18
La Col-A	12 (100%)			12
Vargas 2A	7 (100%)			7
Olmo Redondo 8	28 (93%)		2 (7%)	30
Olmo Redondo 5	14 (88%)		2 (13%)	16
Vargas 3	22 (100%)			22
Vargas 1A	63 (97%)	2 (3%)		65
Vargas 4BB	24 (96%)		1 (4%)	25
Vargas 4B	7 (100%)			7
Vargas 4A	36 (97%)	1 (3%)		37
Olmo Redondo 4A	7 (78%)		2 (22%)	9
San Roque 3	1 (50%)		1 (50%)	2
Artesilla	129 (98%)	2 (2%)	1 (1%)	132

Table 23. Lingual Anterolophid m2

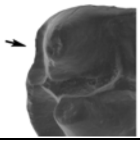
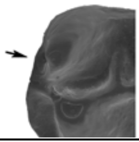
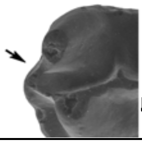
Localities				N
Valdemoros 1A	1 (3%)	28 (93%)	1 (3%)	30
Valdemoros 8A		3 (100%)		3
Moratilla 3		1 (100%)		1
Moratilla 2		1 (100%)		1
Fuente Sierra 4	1 (20%)	3 (60%)	1 (20%)	5
La Retama	19 (23%)	55 (66%)	9 (11%)	83
La Col-D	10 (22%)	32 (70%)	4 (9%)	46
La Col-C	16 (28%)	41 (71%)	1 (2%)	58
La Col-B		4 (100%)		4
Valtorres (type material+MNCN)	12 (25%)	35 (73%)	1 (2%)	48
Valtorres type Material	8 (27%)	21 (70%)	1 (3%)	30
Valtorres extra type Material	2 (50%)	2 (50%)		4
Valtorres MNCN	2 (14%)	12 (86%)		14
Fuente Sierra 3	2 (17%)	10 (83%)		12
Fuente Sierra 2	1 (17%)	5 (83%)		6
Vargas 2B	1 (9%)	9 (82%)	1 (9%)	11
Olmo Redondo 9	2 (11%)	13 (72%)	3 (17%)	18
La Col-A	1 (11%)	8 (89%)		9
Vargas 2A	5 (45%)	6 (55%)		11
Olmo Redondo 8	8 (26%)	19 (61%)	4 (13%)	31
Olmo Redondo 5	4 (36%)	6 (55%)	1 (9%)	11
Vargas 3	8 (36%)	11 (50%)	3 (14%)	22
Vargas 1A	13 (20%)	49 (74%)	4 (6%)	66
Vargas 4BB	10 (38%)	16 (62%)		26
Vargas 4B	2 (33%)	4 (67%)		6
Vargas 4A	20 (47%)	21 (49%)	2 (5%)	43
Olmo Redondo 4A	7 (54%)	6 (46%)		13
San Roque 3	2 (100%)			2
Artesilla	27 (24%)	77 (69%)	8 (7%)	112

Table 24. Mesolophid m2

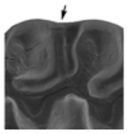
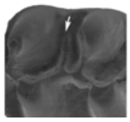
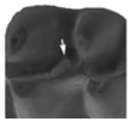
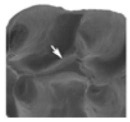
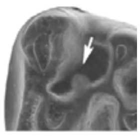
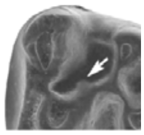
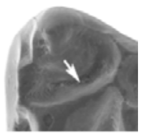
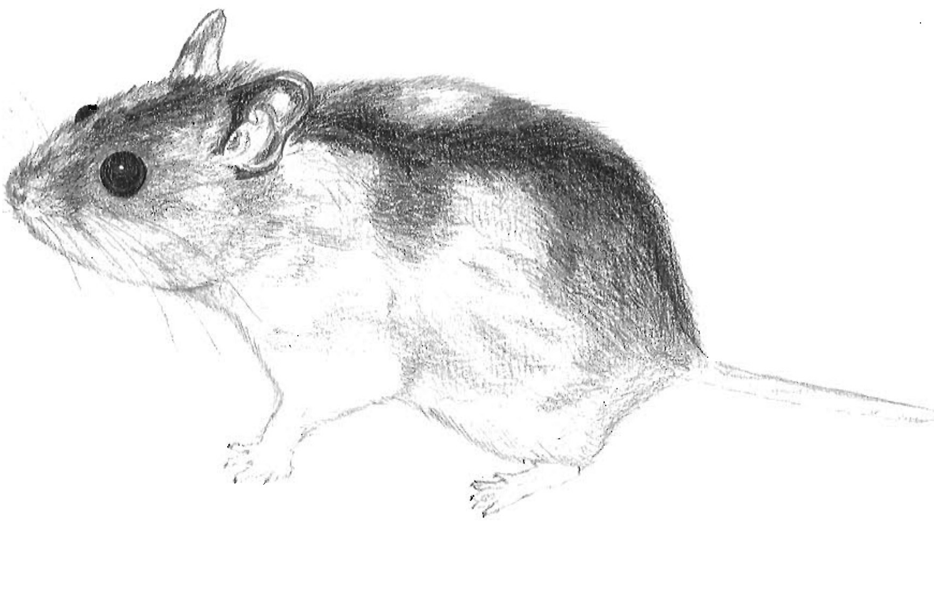
Localities					N
Valdemoros 1A		1 (3%)	24 (77%)	6 (19%)	31
Valdemoros 8A			5 (83%)	1 (17%)	6
Moratilla 3		1 (100%)			1
Moratilla 2				1 (100%)	1
Fuente Sierra 4			5 (100%)		5
La Retama		2 (2%)	69 (74%)	22 (24%)	93
La Col-D	1 (2%)	3 (6%)	37 (73%)	10 (20%)	51
La Col-C	1 (2%)	16 (24%)	39 (59%)	10 (15%)	66
La Col-B			3 (60%)	2 (40%)	5
Valtorres (type material+MNCN)		6 (12%)	37 (73%)	8 (16%)	51
Valtorres type Material		6 (18%)	23 (68%)	5 (15%)	34
Valtorres extra type Material			3 (100%)		3
Valtorres MNCN			11 (79%)	3 (21%)	14
Fuente Sierra 3			13 (93%)	1 (7%)	14
Fuente Sierra 2			9 (100%)		9
Vargas 2B			14 (93%)	1 (7%)	15
La Col-A		2 (17%)	8 (67%)	2 (17%)	12
Vargas 2A		2 (15%)	7 (54%)	4 (31%)	13
Olmo Redondo 8		6 (16%)	28 (74%)	4 (11%)	38
Olmo Redondo 5		1 (8%)	8 (67%)	3 (25%)	12
Vargas 3		5 (19%)	15 (58%)	6 (23%)	26
Vargas 1A	1 (1%)	3 (4%)	63 (84%)	8 (11%)	75
Vargas 4BB		3 (11%)	15 (56%)	9 (33%)	27
Vargas 4B		1 (14%)	5 (71%)	1 (14%)	7
Vargas 4A	1 (2%)	8 (17%)	29 (60%)	10 (21%)	48
Olmo Redondo 4A		3 (21%)	11 (79%)		14
San Roque 3			2 (100%)		2
Artesilla	2 (2%)	38 (31%)	67 (55%)	14 (12%)	121

Table 25. Mesolophid m3

Localities				N
Valdemoros 1A			11 (100%)	11
Valdemoros 8A	1 (8%)		11 (92%)	12
Fuente Sierra 4	1 (50%)		1 (50%)	2
La Retama			8 (100%)	8
La Col-D			2 (100%)	2
La Col-B			2 (100%)	2
Valtorres (type material+MNCN)	4 (20%)	1 (5%)	15 (75%)	20
Valtorres type Material	4 (25%)	1 (6%)	11 (69%)	16
Valtorres extra type Material			1 (100%)	1
Valtorres MNCN			3 (100%)	3
Fuente Sierra 2			1 (100%)	1
Vargas 2B			2 (100%)	2
Vargas 2A			2 (100%)	2
Olmo Redondo 8	1 (20%)		4 (80%)	5
Olmo Redondo 5			3 (100%)	3
Vargas 1A	1 (6%)		16 (94%)	17
Vargas 4BB			4 (100%)	4
Vargas 4B			1 (100%)	1
Olmo Redondo 4A	1 (20%)		4 (80%)	5
Vargas 4A			1 (100%)	1
Artesilla			36 (100%)	36

5. *Megacricetodon alvarezae* sp. nov.



5.1. INTRODUCTION

In this chapter, and in the following two, we will study the *Megacricetodon* material from localities in the Calatayud-Montalbán Basin that different authors have assigned to *M. collongensis* (Daams & Freudenthal, 1988a; Daams et al., 1999a), excluding the material, discussed on the previous chapter, assigned to *M. primitivus* (see Table 5.1).

The first author to work with the *Megacricetodon* material from the Calatayud-Montalbán was Freudenthal (1963). This author assigned to *M. collongensis* the Spanish material from the localities of Valdemoros 3B, Villafeliche 4, Las Planas 4A, Las Planas 4B, Torralba 1, and Armantes 1. Afterwards, Daams & Freudenthal (1988a) in their work about the Iberian *Megacricetodon* corroborated the idea of Freudenthal (1963) and considered that *Megacricetodon collongensis* occurred in the middle Miocene of the Iberian Peninsula, France and Central Europe. According to them, this species would have kept constant through time and without significant differences between one area and another. The distribution of this species is, according to Daams & Freudenthal (1988a) from middle zone D1 to zone E. On the contrary Aguilar (1980; 1995) considers that the *Megacricetodon* material from the Iberian Peninsula must be assigned to a different species than to *Megacricetodon collongensis* from France. According to Aguilar (1995), the Iberian and the French lineages evolved independently since they belong to different biogeographic provinces.

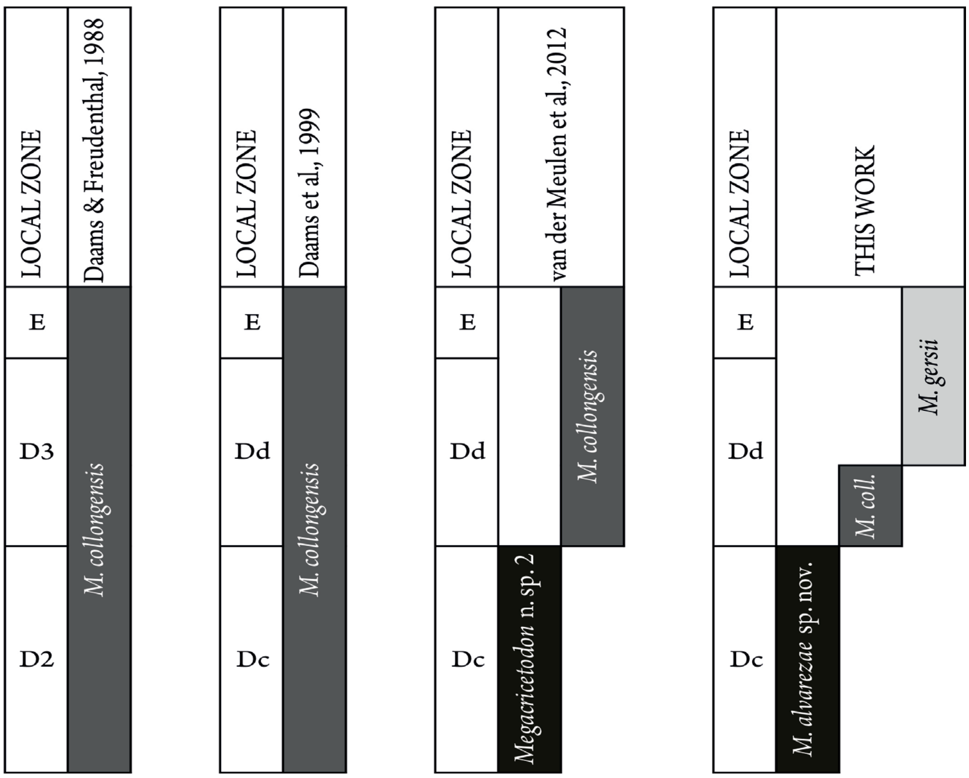


Table 5.1. History of the species *M. collongensis* in the Calatayud-Montalbán Basin

As will be demonstrated in this work, the material included in *M. collongensis* by Daams & Freudenthal (1988a) and Daams et al. (1999a) show important morphological differences , and therefore we consider that some of the Spanish associations must be assigned to different species. Table 5.1 shows the changes on the taxonomical ideas by different authors about the *Megacricetodon* material from the Calatayud-Montalbán Basin. As a result of this work we propose that, throughout the middle Aragonian three species of *Megacricetodon* occurred. The first of these species is *Megacricetodon alvarezae* sp. nov., a new species which occurs in the local zone Dc (in this chapter we focus on this species). The second one is the small *M. collongensis* which occurs in the lower part of the biozone Dd. And the third one is the large-sized *M. gersii* which occurs in the lowermost part of local zone Dd and E (Chapter 6).

Thus, Aguilar (1980; 1995) interpreted correctly some of the differences between the Spanish and French material, considering that he compared the French material of *M. collongensis* with the Spanish *Megacricetodon* from the localities Valdemoros 3B and Villafeliche 4 (in the local zone Dc) now considered as a new species, and from Las Planas 4 localities (uppermost part of local zone Dd), now considered also as different to *M. collongensis*, as will be discussed in chapter 7. Consequently, only a limited amount of the *Megacricetodon* material from localities in the Calatayud-Montalbán Basin are now assigned to *M. collongensis*. The distribution of this species is along the lower part of local zone Dd, as will be discussed in the next chapter.

Therefore, this chapter summarizes the results on a new species of *Megacricetodon* based on new and already known material from localities in the Calatayud-Montalban Basin included in the local zones Db and Dc.

Objectives of the chapter:

- Describe and define the *Megacricetodon* species characteristic of the local zone Dc.
- Discuss the relative position of the localities of the local zone Dc from the Calatayud-Montalbán Basin.
- Determine the temporal and geographic distribution of the species in Europe.

5.2. MATERIAL

Megacricetodon alvarezae sp. nov. has been recovered from the well-known Spanish basin of Calatayud-Montalbán (Daams et al., 1999b; van der Meulen et al., 2011; 2012). We included eight localities of this basin: Munébrega 3A, Valdemoros 9, Valdemoros 11, Vargas 5 and Vargas 6, which are stored at the Museo Nacional de Ciencias Naturales, CSIC (Madrid, Spain). Villafeliche 4A, Villafeliche 4B and part of the material from Valdemoros 3B are stored in the collections of the Faculty of Earth Sciences in the University of Utrecht (Utrecht, The Netherlands). And part of the material from Valdemoros 3B which is stored in the Nationaal Natuurhistorisch Museum-Naturalis (Leiden, The Netherlands).

Other material studied and compared with the Calatayud-Montalbán assemblages are: (1) From Spanish basins: *M. lopezae* García-Moreno (en Álvarez-Sierra & García-Moreno, 1986), from Simancas 2; *M. primitivus* from Valtorres; *M. rafaeli* Daams & Freudenthal, 1988a, from Armantes 7; and *M. vandermeuleni* from La Col D, La Retama, Fuente Sierra 4, Moratilla 2, Moratilla 3 and Valdemoros 8A; (2) From French basins: *M. bezianensis* from, Bézian; *M. bourgeoisi* from Suèvres; *M. collongensis* from Vieux-Collonges; *M. gersii* from Sansan; and *M. lalai* from Châteauredon; (3) *M. similis* (Fahlbusch, 1964) from Giggenhausen (Germany); (4) *M. minutus* Daxner, 1967 from Inzersdorf (Austria); (5) *M. crisiensis* Radulescu & Samson, 1988, from Comãnesti-1 (Romania); (6) From Pakistan: *Megacricetodon aguilari* Lindsay, 1988, *M. daamsi* Lindsay, 1988 and *M. sivalensis* Lindsay, 1988; (7) *Megacricetodon andrewsi* Peláez-Campomanes & Daams, 2002 from Paşalar (Turkey); (8) From China: *M. beijiangensis* Maridet et al., 2011 from the locality of XJ 200114; *M. sinensis* Qiu et al., 1981 from Danshuilu; and *M. yei* Bi et al, 2008 from Tieersihabahe.

5.3. SYSTEMATIC PALAEONTOLOGY

Order RODENTIA Bowdich, 1821
Family MURIDAE Illiger, 1811
Subfamily CRICETODONTINAE Schaub, 1925
Genre MEGACRICETODON Fahlbusch, 1964
MEGACRICETODON ALVAREZAE sp. nov.
(Figs. 5.1 A–Z)

Cricetodon minor collongensis from Valdemoros 3B and Villafeliche IV in Freudenthal, 1963: 28-32.

Megacricetodon collongensis pro-parte from Valdemoros 3B, Villafeliche 4A and Villafeliche 4B in Daams and Freudenthal, 1988a.

Megacricetodon primitivus-collongensis pro-parte from D1 in van der Meulen and Daams, 1992: 231, fig. 1.

Megacricetodon collongensis from Dc in Daams et al., 1998: 627, fig. 1.

Megacricetodon collongensis from Dc in Daams et al., 1999a: 126, fig. 10, 127.

Megacricetodon collongensis from Dc in Alcalá et al., 2000: 327, fig. 3.

Megacricetodon collongensis Herráez et al., 2006: 261.

Megacricetodon collongensis pro-parte from Dc in Sesé, 2006: 440.

Megacricetodon n. sp. 2 van der Meulen et al., 2012: 166, figs. 3, 4, 6.

Megacricetodon nov. sp. Oliver & Peláez-Campomanes, 2013: 953, fig. 10.

Diagnosis: Medium-sized species of *Megacricetodon* (M1 mean length <1,65 mm, m1 mean length <1,50 mm). Lower first molar with well-individualized anteroconid (conical-shaped anteroconid and low anterolophids that only reaches the base of the anteroconid); the anteroconid is double between the 20-50% of the specimens; occassionaly shows an antero-lingual and antero-labial cingulid and a labial spur of the anterolophulid; long anterolophulid; ectomesolophid absent; mesolophids of short length in m1 and m2. Upper first molar with an anterocone always double, normally with a platform in front of it; there is a strong lingual mesocingulum that connects the hypocone to the anterocone in more than 20% of the specimens; mesoloph normally short.

Differential Diagnosis: *Megacricetodon alvarezae* sp. nov. differs from the small-sized group of *Megacricetodon* defined by Peláez-Campomanes & Daams (2002) and Oliver & Peláez-Campomanes (2013) by its larger dimensions.

Megacricetodon alvarezae sp. nov. differs from the large-sized group of *Megacricetodon* by its significantly smaller dimensions.

Due to the medium size of our species, we compared it with the medium-size group of *Megacricetodon* defined by Peláez-Campomanes & Daams (2002) and Oliver & Peláez-Campomanes (2013):

Megacricetodon aguilari Lindsay, 1988 differs from the new species by its larger size.

Megacricetodon andrewsi Péláez-Campomanes & Daams, 2002, *M. bourgeoisi* (Schaub, 1925), *M. crisiensis* Radulescu & Samson, 1988, *M. daamsi* Lindsay, 1988, *M. lalai* Aguilar, 1999, *M. lopezae* García-Moreno (in Álvarez-Sierra & García-Moreno, 1986), *M.*

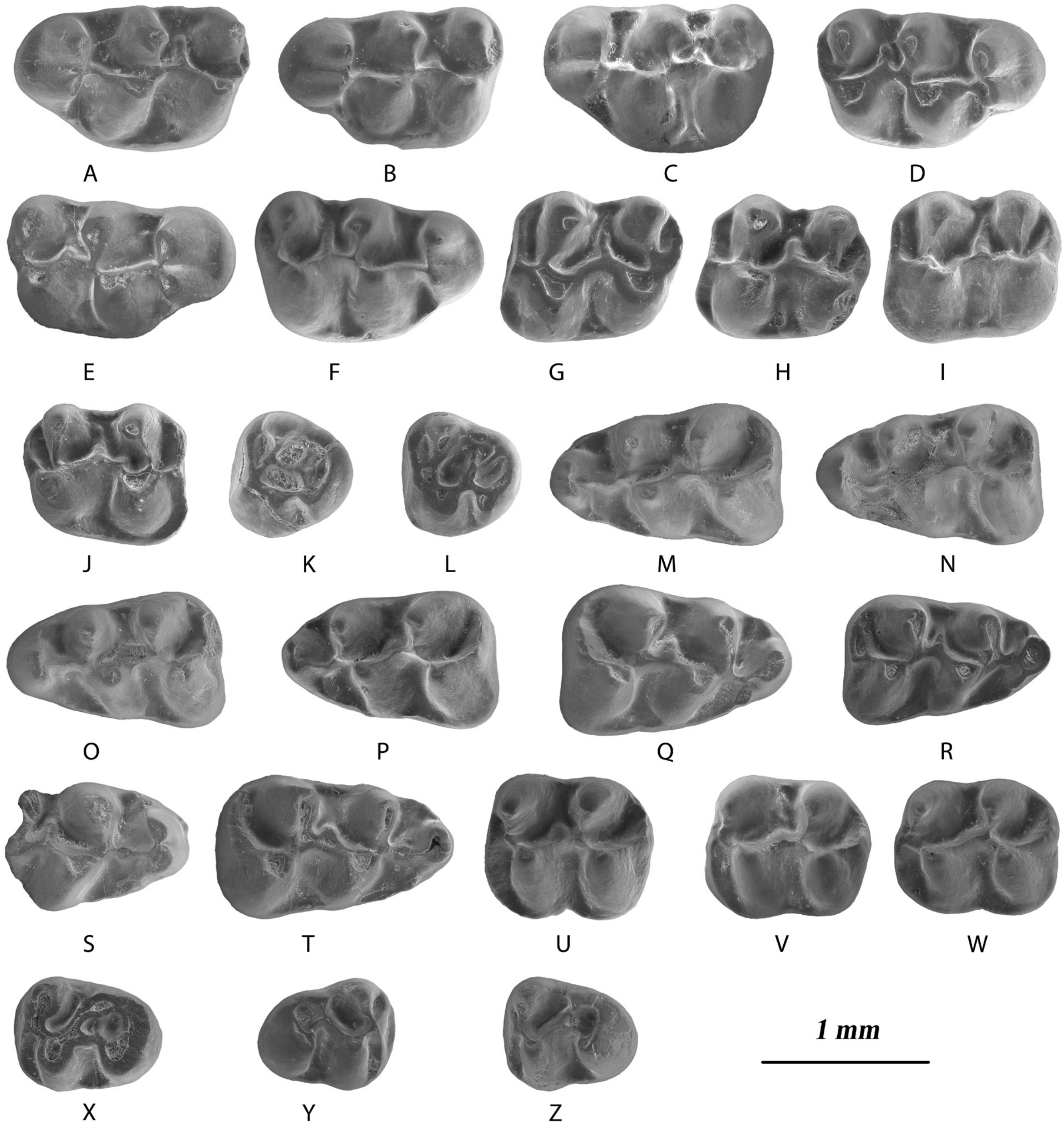


Figure 5.1. *Megacricetodon alvarezae* sp. nov. from type locality Vargas 6. A, VR6-254 M1 left; B, VR6-274 M1 left; C, VR6-274 M1 left; D, VR6-280 M1 right; E, VR6-289 M1 right; F, VR6-290 M1 right; G, VR6-300 M2 left; H, VR6-303 M2 left; I, VR6-314 M2 left; J, VR6-324 M2 right; K, VR6-2.0 M3 left; L, VR6-3.4 M3 left; M, holotype VR6-343 m1 left; N, VR6-348 m1 right; O,VR6-355 m1 left; P,VR6-359 m1 left; Q, VR6-370 m1 right; R, VR6-372 m1 right; S, VR6-377 m1 left; T, VR6-381 m1 right; U, VR6-384 m2 left; V, VR6-385 m2 left; W, VR6-388 m2 left; X, VR6-1.4 m3 left; Y, VR6-4.6 m3 right; Z, VR6-5.0 m3 left. All of the teeth are at the same magnification. Scale bar equals 1 mm.

minutus Daxner, 1967, *M. rafaeli* Daams & Freudenthal, 1988a and *M. similis* (Fahlbusch, 1964) are similar in size to *M. alvarezae* sp. nov. but differs by having less subdivided the anterocone of the upper first molar.

Megacricetodon alvarezae sp. nov. is similarly sized to the Asiatic *Megacricetodon* species (*M. beijiangensis* Maridet et al., 2011, *Megacricetodon sinensis*, Qiu et al., 1981, *M. sivalensis* Lindsay, 1988, *M. yei* Bi et al, 2008), however, differs by having the anteroconid of the m1 well individualized, with conical shaped anteroconid and low anterolophids that only reaches the base of the anteroconid, and shorter mesolophs in M1 and M2.

Megacricetodon gersii Aguilar, 1980 from Sansan, differs from the new species by having a higher percentage of double anteroconid with a labial anterolophid that reaches the top of the anteroconid.

The species included in the *Megacricetodon bavaricus* group (*M. aunayi* Lazzari & Aguilar, 2007, *M. bavaricus* Fahlbusch, 1964, *M. bezianensis* Bulot, 1980 and *M. vandermeuleni* Oliver & Peláez-Campomanes, 2013) differs from *Megacricetodon alvarezae* sp. nov. by the slightly subdivided anterocone in the upper first molar and the characteristic "crescent"-shape anteroconid in the lower first molar.

We have also compared this new species with two small-sized *Megacricetodon*: *M. collongensis* (Mein, 1958) from Vieux-Collonges differs from *M. alvarezae* sp. nov., by having ectoloph always present in the M1 and M2, high labial anterolophid in the m1, and different proportions between the m1 and the m3 (being shorter the m1 and bigger the m3 in *M. collongensis*).

Megacricetodon primitivus (Freudenthal, 1963) differs from the new species, by the smaller size, more robust teeth, higher anterolophids and less individualized anteroconid in the m1, and longer mesoloph(id) in the M2, m1 and m2.

Holotype: m1 left, VR6-343 (Fig. 5.1 M).

Etymology: Dedicated to our colleague and friend Dr. M. A. Álvarez Sierra.

Type Locality: Vargas 6, province of Zaragoza, Calatayud-Montalbán Basin, Spain.

Paratypes: VR6-253 to VR6-299, VR6-326 to VR6-428, VR6-434, VR6-435, VR6-438, VR6-445, VR6-451, VR6-456, VR6-460, VR6-464, VR6-466, VR6-469, VR6-475, VR6-476, VR6-482, VR6-490, VR6-496, VR6-499, VR6-500, VR6-504 to VR6-507, VR6-509, VR6-510, VR6-519, VR6-520, VR6-526, VR6-533, VR6-540, VR6-546, VR6-548, VR6-554, VR6-556, VR6-559, VR6-560, VR6-565, VR6-566, VR6-575, VR6-576.

Other Localities From the Calatayud-Montalbán Basin: Vargas 5, Valdemoros 9, Valdemoros 11, Valdemoros 3B, Villafeliche 4A, Villafeliche 4B, from the Aragonian type area (Zaragoza); and Munébrega 3A from the Calatayud area (Zaragoza) (Fig. 5.2).

Stratigraphical distribution: Uppermost part of local zone Db and local zone Dc (van der Meulen et al., 2012), middle Aragonian, middle Miocene.

Geographical distribution: Iberian Peninsula (Spain and Portugal).

Measurements: Table 5.2.

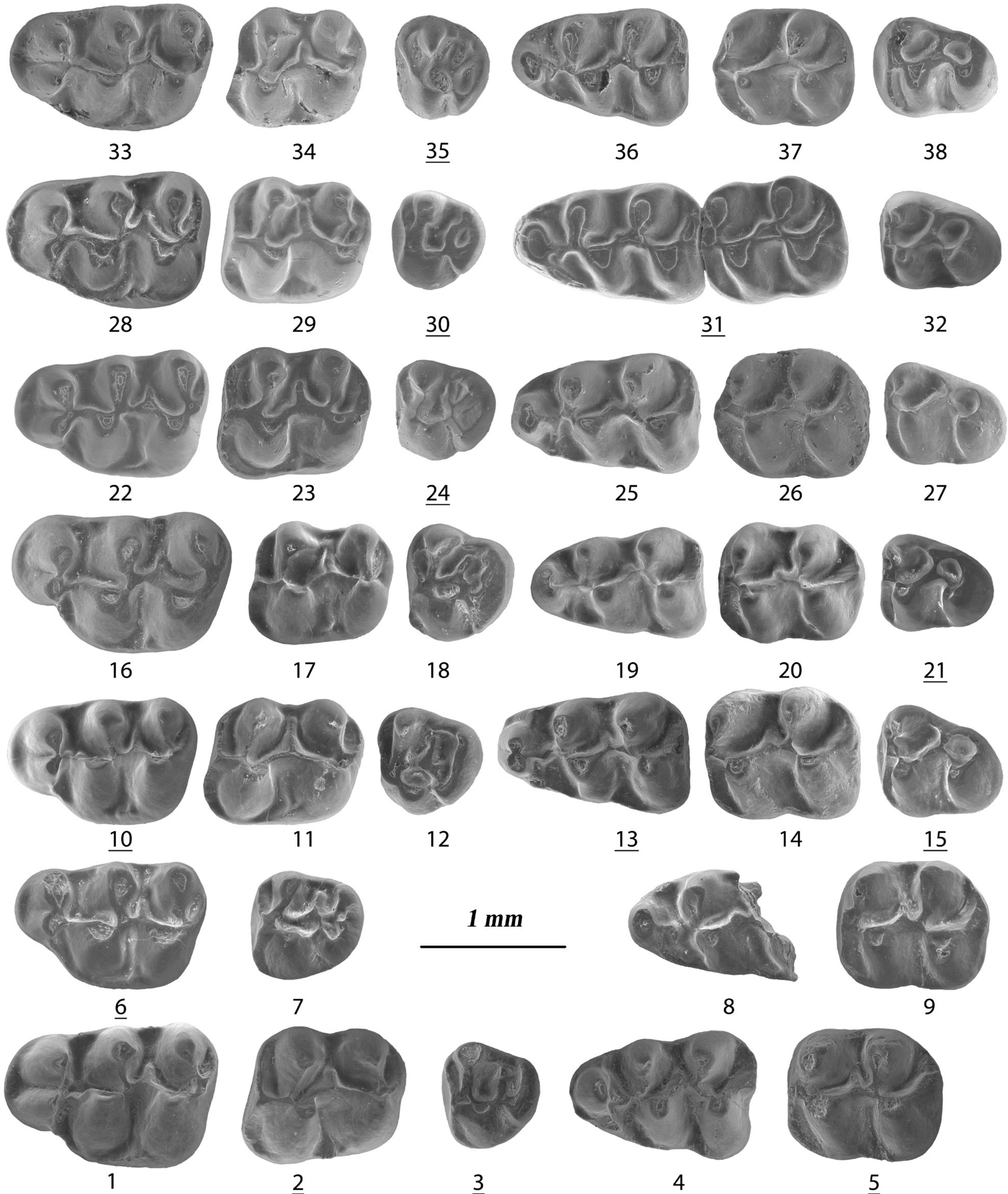


Figure 5.2. *Megacricetodon alvarezae* sp. nov. from other localities of the Calatayud-Montalbán Basin. From Munébrega 3A: 1, MUN3A-15 M1 left; 2, MUN3A-5.3 M2 right; 3, MUN3A-9.7 M3 right; 4, MUN3A-3.6 m1 left; 5, MUN3A-7.9 m2 right; From Valdemoros 9: 6, VA9-11 M1 right; 7, VA9-15 M3 left; 8, VA9-12 m1 left; 9, VA9-13 m2 left; From Vargas 5:10, VR5-3 M1 right; 11, VR5-7 M2 left; 12, VR5-3.0 M3 left; 13, VR5-257 m1 right; 14, VR5-270 m2 left; 15, VR5-412 m3 right; From Valdemoros 11: 16, VA11-3 M1 left; 17, VA11-14 M2 left; 18, VA11-28 M3 left; 19, VA11-30 m1 left; 20, VA11-35 m2 left; 21, VA11-45 m3 right; From Valdemoros 3B: 22, VA3B-1135 M1 left; 23, VA3B-1172 M2 left; 24, VA3B-1232 M3 right; 25, VA3B-1029 m1 left; 26, VA3B-1051 m2 left; 27, VA3B-1092 m3 left; From Villafeliche 4A: 28, VL4A-3.4 M1 left; 29, VL4A-254.175 M2 left; 30, VL4A-254.196 M3 right; 31, VL4A-1.0 mandible m1-m2 right; 32, VL4A-254.129 m3 left; From Villafeliche 4B: 33, VL4B-1021 M1 left; 34, VL4B-1034 M2 left; 35, VL4B-1045 M3 right; 36, VL4B-4.2 m1 left; 37, VL4B-1010 m2 left; 38, VL4B-1018 m3 left. Right side specimens underlined. All of the teeth are at the same magnification. Scale bar equals 1 mm.

Element	Sites	Length						Width				
		T. N.	N.	min	mean	max	σ	N.	min	mean	max	σ
M1	VL4B	18	14	1,41	1,54	1,65	0,060	15	0,90	0,97	1,06	0,040
	VL4A	75	37	1,41	1,54	1,68	0,060	45	0,89	0,97	1,05	0,040
	VA3B	44	33	1,44	1,52	1,63	0,05	37	0,91	1	1,1	0,04
	VA11	11	7	1,39	1,55	1,69	0,09	8	0,89	1	1,08	0,06
	VR6	46	18	1,42	1,52	1,63	0,050	30	0,92	0,98	1,07	0,040
	VR5	34	13	1,51	1,60	1,69	0,060	21	0,91	1,02	1,14	0,060
	VA9	1	1		1,42			1		0,96		
	MUN3A	27	16	1,52	1,63	1,72	0,060	18	0,95	1,05	1,14	0,050
M2	VL4B	25	15	1,02	1,08	1,15	0,040	13	0,88	0,93	1,01	0,040
	VL4A	60	45	0,98	1,08	1,16	0,040	44	0,88	0,95	1,04	0,040
	VA3B	55	39	1,01	1,1	1,18	0,05	37	0,89	0,96	1,03	0,04
	VA11	19	12	1,02	1,11	1,23	0,060	12	0,88	0,96	1,06	0,050
	VR6	46	26	1,03	1,11	1,18	0,050	26	0,86	0,97	1,05	0,050
	VR5	26	17	1,04	1,14	1,26	0,050	18	0,95	1,00	1,09	0,040
	MUN3A	30	20	1,11	1,17	1,26	0,050	21	0,91	1,02	1,09	0,050
M3	VL4B	5	5	0,68	0,70	0,71	0,010	5	0,72	0,76	0,79	0,030
	VL4A	3	2	0,65	0,68	0,71	0,04	2	0,71	0,72	0,73	0,01
	VA3B	29	20	0,64	0,74	0,85	0,05	20	0,69	0,78	0,87	0,04
	VA11	1	1		0,83			1		0,88		
	VR6	9	7	0,73	0,77	0,81	0,04	7	0,76	0,8	0,85	0,04
	VR5	4	2	0,77	0,78	0,79	0,010	2	0,81	0,84	0,86	0,040
	VA9	1	1		0,82			1		0,80		
	MUN3A	7	4	0,71	0,78	0,83	0,050	6	0,77	0,83	0,88	0,050
m1	VL4B	23	14	1,29	1,38	1,48	0,050	17	0,81	0,87	0,91	0,040
	VL4A	88	48	1,27	1,39	1,52	0,060	62	0,81	0,88	0,97	0,040
	VA3B	39	25	1,29	1,42	1,53	0,06	28	0,83	0,9	0,95	0,03
	VA11	11	5	1,33	1,41	1,49	0,070	7	0,85	0,89	0,94	0,030
	VR6	40	15	1,33	1,42	1,56	0,070	22	0,84	0,89	0,94	0,030
	VR5	25	13	1,44	1,48	1,55	0,030	20	0,88	0,92	0,97	0,030
	MUN3A	29	15	1,41	1,49	1,56	0,050	20	0,82	0,94	1,09	0,050
	VA8A	4	4	1,44	1,5	1,53	0,04	4	0,91	0,92	0,93	0,01
m2	VL4B	15	8	1,01	1,08	1,12	0,030	8	0,85	0,92	0,98	0,040
	VL4A	75	57	0,99	1,08	1,15	0,030	59	0,84	0,92	0,98	0,030
	VA3B	51	37	0,98	1,09	1,17	0,04	39	0,84	0,93	1	0,04
	VA11	8	7	1,01	1,12	1,21	0,060	7	0,89	0,94	0,98	0,030
	VR6	48	26	1,05	1,11	1,19	0,03	27	0,9	0,94	1,03	0,03
	VR5	36	18	1,05	1,15	1,23	0,040	23	0,90	0,98	1,03	0,040
	VA9	1	1		1,14			1		0,98		
	MUN3A	27	13	1,11	1,15	1,20	0,020	16	0,90	0,99	1,09	0,050
m3	VL4B	4	4	0,85	0,90	0,93	0,040	3	0,74	0,75	0,76	0,010
	VL4A	5	5	0,81	0,88	0,91	0,040	5	0,75	0,77	0,79	0,020
	VA3B	33	22	0,74	0,86	0,93	0,05	25	0,69	0,75	0,8	0,03
	VA11	4	4	0,81	0,85	0,90	0,040	4	0,71	0,74	0,76	0,020
	VR6	13	8	0,84	0,90	0,97	0,050	8	0,74	0,78	0,85	0,040
	VR5	7	5	0,88	0,92	0,97	0,040	5	0,77	0,80	0,83	0,020
	MUN3A	13	8	0,94	1	1,06	0,04	10	0,76	0,81	0,87	0,04

Table 5.2. Descriptive statistics of the upper and lower molars of *Megacricetodon alvarezae* nov. sp. from the Calatayud-Montalbán Basin. Abbreviations: T.N., total number of teeth; N., number of teeth measured; min, minimum; max, maximum; δ, standard deviation.

5.4. DESCRIPTION OF THE TYPE MATERIAL

M1: The anterocone is deeply split in most specimens (25/27), of which 22 have a small platform in front of the furrow. In the remaining two, the anterocone is slightly subdivided with a small platform in front of the furrow. In 31 out of 34 teeth the labial cone of the anterocone is larger than the lingual; in the remaining three, both present equal size. The anterolophule is connected to the lingual cone of the anterocone (19/36), to the labial cone (2/36) or between the two lobes of the anterocone (15/36). In 11 out of 44 there is a short labial spur of the anterolophule, in three out of 44 is incipient and in 30 out of 44 is absent. The protolophule is posterior (34/41), posterior almost double (5/41) or double (2/41). The ectoloph is short in 28, and absent in 10. A lingual mesocingulum that connects the protocone to the hypocone, is present in 12 out of 40 specimens. The mesoloph is medium (12/41) or short (29/41). The ectoloph is connected with the mesoloph in 1 out of 38, in 26 there is no connection between the ectoloph and the mesoloph, and in 11 there is a mesoloph but the ectoloph is absent. The metalophule is posterior and the metalophule points backwards (28/30), or is posterior and the metalophule points backwards more obliquely delimiting a small posterosinus (2/30). (See Appendix 5.1 Table 1-10).

M2: The protolophule is anterior in 26 specimens, is anterior almost double in four, is transverse in four, and it is double in one. The ectoloph is strong (2/41) short (32/41) or absent (7/41). Only one specimen (1/39) has a lingual mesocingulum that connects the protocone with the hypocone. The mesoloph is long in one, medium in 18 and short in 23 specimens. The ectoloph is connected with the mesoloph in two, there is no connection between the ectoloph and the mesoloph in 31, and there is a mesoloph but the ectoloph is absent in seven. The metalophule is anterior (25/33), transverse (2/33), points backwards and it is connected to the posteroloph, just behind the hypocone (4/33), the metalophule is more oblique reducing the posterosinus (1/33) or double (1/33). (Appendix 5.1 Table 11-16).

M3: The lingual anterolophule is well developed in two, is incipient in two, and absent in five. The protolophule is always anterior and the paracone is always well developed. The mesoloph is present in eight specimens (8/9). In six out of nine, the metalophule is connected to the neo-entoloph, in one the metalophule is connected to the anterior arm of the hypocone, and in two the metalophule is connected to the anterior arm of the hypocone and the protolophule. (See Appendix 5.1 Table 17).

m1: The anteroconid is rounded, being simple in 18 specimens, slightly subdivided in eight and 8-shaped in four. The lingual and labial anterolophids have a low height and therefore the anteroconid is individualized. 1 out of 27 specimens have an antero-lingual cingulid, and four out of 27 have a slight anterior depression. Only one specimen (1/32) has an antero-labial cingulid. A labial spur of the anterolophulid is present in nine specimens, incipient in three and absent in 25. The metalophulid is anteriorly connected in 32 specimens (32/36), is anteriorly connected with a second connection almost complete in two, and is disconnected in two. The mesolophid is medium (3/35), short (28/35) or absent (4/35). (Appendix 5.1 Table 18-22).

m2: The lingual anterolophulid is long in two out of 41 specimens, short in 33 and absent in six. Two specimens have a double metalophulid. The mesolophid is medium (1/46) short (40/46) or absent (5/46). The hypolophulid is always anterior. (See Appendix 5.1 Table 23-24).

m3: The lingual anterolophulid is short in eight specimens and absent in the remaining one. In four specimens there is a small crest connecting the ectolophid with the entoconid. The mesolophid is always absent. (Appendix 5.1 Table 25-26).

5.5. DISCUSSION

Megacricetodon alvarezae sp. nov. is, morphologically, an homogeneous species from its first occurrence in local zone Db (~15.68 Ma) to its last occurrence in local zone Dc (~14.830 Ma). Through this time period, the new species exhibits a slightly decrease in size, see Table 5.2, but keeping constant its dental morphology.

The combination of morphological characters of *M. alvarezae* sp. nov. (lower first molar with conical-shaped anteroconid and low anterolophids that only reaches the base of the anteroconid, double anteroconid between the 20-50% of the specimens, low anterolophids and occassionaly with an anterior cingulid and a labial spur of the anterolophulid; and upper molars with an anterocone always double, normally with a platform in front of the furrow, an a strong lingual mesocingulum that connects the hypocone to the anterocone in more than 20% of the specimens), allow us to differentiate it from other *Megacricetodon* species.

The different assemblages of *M. alvarezae* sp. nov. from Calatayud-Montalbán Basin are morphologically very similar. Nevertheless, material from some localities shows small differences with the type material of Vargas 6. The material from Vargas 5 has longer ectoloph and mesoloph in the upper first molars, the connection between the mesoloph and the ectoloph is more frequent in the M2, and the lower first molar has higher percentage of metalophule double or almost double (Appendix 5.1 Tables 6, 7, 15, 20). The material from the localities of VL4A and VL4B, show a higher percentage of lingual mesocingulum that connects the hypocone to the anterocone in the M1 (Appendix 5.1 Table 8). Finally, the differences in the character distribution with the assemblage of Valdemoros 9 could be due to scarcity of the material from this locality.

The site of Valdemoros 8A (VA8A), also located in the Calatayud-Montalbán Basin, is an older locality belonged to the local zone Db (middle Aragonian, middle Miocene). This site contains three species of *Megacricetodon*: *M. primitivus*, *M. vandermeuleni* (Oliver & Peláez-Campomanes, 2013) and *M. alvarezae* sp. nov. Like Munébrega 3A and Vargas 5, the specimens of *M. alvarezae* sp. nov. from Valdemoros 8A are larger than those from the rest of the localities (see Table 5.1).

With regard to the size, and to test significant differences among the assemblages of *Megacricetodon alvarezae* sp. nov. from Calatayud-Montalbán Basin we carried out analysis of variance (ANOVA) and post hoc tests (Appendix 5.2). The statistical analyses showed that there are significant differences in size between the *Megacricetodon* from the oldest localities of the local zone Dc (MUN3A and VR5), and the *Megacricetodon* from the youngest localities of the zone (Appendix 5.2 Tables 2-5). *Megacricetodon alvarezae* sp. nov. from Munébrega 3A and Vargas 5, are larger than the rest of the localities, suggesting a reduction of size within this zone (Table 5.2 and Figure 5.3). However, despite these differences in size, the morphology remains rather constant in all the assemblages (see Appendix 5.1) and therefore we prefer to consider all those assemblages as belonging to the same species.

Megacricetodon alvarezae sp. nov. not only occurs in the Calatayud-Montalbán Basin, other European basins also have this new species:

In the Madrid Basin, the *Megacricetodon* material from the locality of Los Nogales was allotted to *M. collongensis* and correlated to local zone Dc (Herráez et al., 2006). However, both the morphology and size of this material is more compatible with *M. alvarezae* sp. nov. instead to *M. collongensis*.

In Portugal, the locality of Chelas 2 (Tagus Basin) was assigned to local zone Dc (Antunes et al., 1996; Antunes, 2000). The scarce material of *Megacricetodon* and the lack of lower first molar, make it difficult to attribute a species, since it could belong (both for the size and for the morphology) to *M. alvarezae* sp. nov. or *M. vandermeuleni*. The occurrence of *Democricetodon* in the Chelas 2, with a similar size to *Democricetodon jordensi*, and an intermediate morphology between *D. moralesi* and *D. jordensi*, suggest that the locality of Chelas 2 was correlated with the lower part of the local zone Dc. Therefore, owing to the scarce *Megacricetodon* material, we proposed its assignation to *Megacricetodon* cf. *alvarezae*.

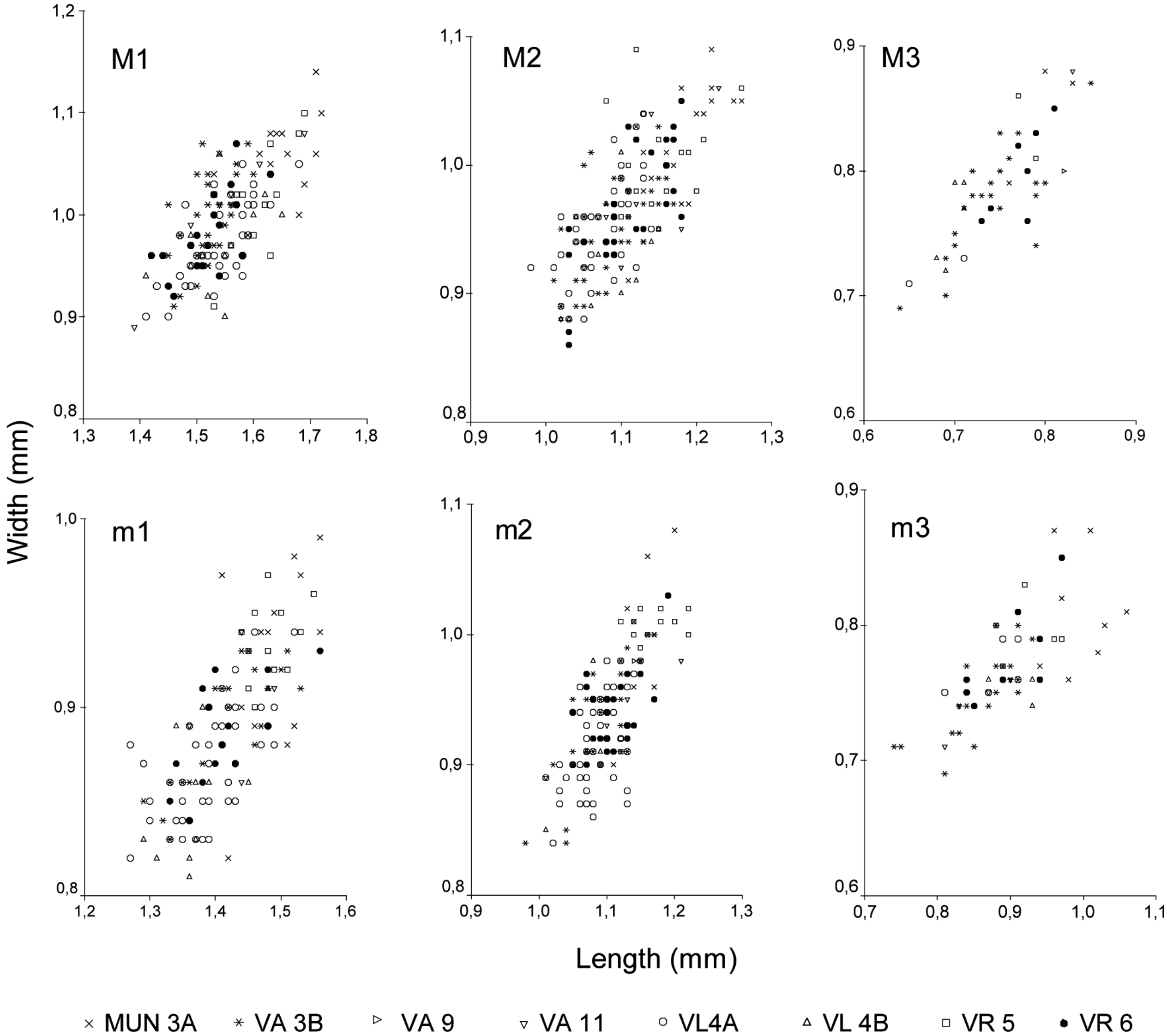


Figure 5.3. Scatter diagram of the measurements of *Megacricetodon alvarezae* nov. sp. from the type locality of Vargas 6 (VR6) and the other assemblages of the zone Dc (MUN3A, VA3B, VA11, VL4A, VL4B and VR5).

In the Calatayud-Montalbán Basin several species with similar size to *M. alvarezae* sp. nov. have been described. *Megacricetodon vandermeuleni* differs by the slightly subdivided anterocone and larger mesoloph in the M1; M2 with lower percentage of protolophule and metalophule double; elongated anteroconid of the m1, lower percentage of metalophulid double of the m1 and a higher percentage of short lingual anterolophulid of the m2.

Up to now, *Megacricetodon* from the local zone Dc was assigned to *M. collongensis* (Daams & Freudenthal 1988a; Daams et al., 1998; Daams et al., 1999a; Alcalá et al., 2000). However, *Megacricetodon alvarezae* sp. nov. differs from *M. collongensis* from Vieux-Collonges, by having conical shaped anteroconid and low anterolophids that only reaches the base of the anteroconid (in contrast *M. collongensis* has high labial anterolophid); the proportions between the m1 and the m3 are different (being shorter the m1 and longer the m3 in *M. collongensis*). *Megacricetodon alvarezae* sp. nov. has also lower percentage of ectolophs present in the M1 and M2.

Megacricetodon primitivus differs from *M. alvarezae* sp. nov., by the smaller size and more robust teeth, lower first molar with high lingual and labial anterolophids, less individualized anteroconid in the m1, lower percentage of double anteroconid, and longer mesolophids in the m1 and m2; M2 with longer ectoloph and mesoloph and a higher percentage of transverse metalophule. Despite those morphometric differences pointed out between the two taxa, the general morphological pattern indicate that *M. alvarezae* sp. nov. is probably closely related to *M. primitivus*.

The small-sized *Megacricetodon primitivus* appeared during the lower part of MN4 in France (localities of Béon 1 and Pellecahus), dispersing through the Iberian Peninsula (Spain and Portugal) in the middle part of MN4. In Spain the first occurrence of *Megacricetodon* is during the local zone Ca, in the locality of Artesilla (Oliver Pérez et al., 2008). This species keeps without much variation (neither the size nor the morphology) till local zone Db, where coexist with *M. vandermeuleni*, a large-sized species which has been related to the French *M. bezianensis* (Oliver & Peláez-Campomanes, 2013), and with *M. alvarezae* sp. nov. (VA8A).

In Portugal, *Megacricetodon primitivus* has been described from the localities of Quinta do Pombeiro and Quinta das Pedreiras, in the lower Aragonian, local zone C (Antunes & Mein, 1971; Antunes, 2000). In the local zone Db, MN5, the locality of Chelas 1 (Aguilar, 1981; Antunes, 2000) occurs a *Megacricetodon* with size of *M. primitivus* but morphology of *M. alvarezae* nov. sp. This intermediate evolutionary stage evolves during local zone Db to a larger-sized *Megacricetodon*. In the locality of Chelas 2, assigned to local zone Dc (Aguilar, 1981; Antunes, 2000) occurs this large-sized *Megacricetodon*, however, owing to the scarce material of this locality, this *Megacricetodon* is preliminary assigned to *M.* cf. *alvarezae*. *Megacricetodon alvarezae* sp. nov., would have entered to Spain from Portugal in the MN5, at the end of the local zone Db (locality of Valdemoros 8A), and dispersing throughout this zone. Being during the local zone Dc the most common species of *Megacricetodon*.

Megacricetodon alvarezae nov. sp. is therefore, an endemic Iberian species, whose population is restricted to the Iberian Peninsula, differentiating this way from other biogeographic provinces.

LOCAL ZONE	Daams et al., 1999	Van der Meulen et al., 2012	THIS WORK	***Megacricetodon* species**		
Dd			Vargas 7	*M. collongensis*		
	Vargas 7	Vargas 7	Valdemoros 3D	*M. collongensis*		
Dc	Valdemoros 3D	Valdemoros 3D	Villafeliche 4B	*M. alvarezae*		
			Villafeliche 4A	*M. alvarezae*		
	Valdemoros 3B	Valdemoros 3B	Valdemoros 3B	*M. alvarezae*		
	Valdemoros 11	Valdemoros 11	Valdemoros 11	*M. alvarezae*		
	Vargas 6	Vargas 6	Vargas 6	*M. alvarezae*		
	Vargas 5	Vargas 5	Vargas 5	*M. alvarezae*		
	Valdemoros 9		Valdemoros 9	*M. alvarezae*		
	Villafeliche 4B	Villafeliche 4B				
	Villafeliche 4A	Villafeliche 4A	Munebrega 3A	*M. alvarezae*	*M. primitivus*	
Db	Valdemoros 8A	Valdemoros 8A	Valdemoros 8A	*M. alvarezae*	*M. primitivus*	*M. vandermeuleni*

Table 5.3. Relative position of the localities of the local zone Dc from the Calatayud-Montalbán Basin

5.6. REMARKS OF THE RELATIVE POSITION OF THE LOCALITIES OF THE LOCAL ZONE Dc FROM THE CALATAYUD-MONTALBÁN BASIN

Based on the material of *Megacricetodon* from the different localities of the local zone Dc, a possible relocation of the localities within the zone is proposed, regarding to what was proposed by Daams et al., (1999a) and van der Meulen et al., (2012). This relocation of the localities coincides with the relative position published for Daams & Freudenthal (1988b) for the zone D2 (See Table 5.3).

The localities of the Vargas section (VR5, VR6 and VR7) are in stratigraphic superposition(Daams et al. 1999a) and therefore have been used as keystone for the proposed changes. The *Megacricetodon* material from VR5 is of large size, whereas the material from the younger locality of VR6 is smaller, being the *Megacricetodon* from VR7 the smallest form.

The localities of Valdemoros 3 (VA3B and VA3D) are also stratigraphically superposed. VA3B is stratigraphically lower and the *Megacricetodon* is of larger size. In contrast, the material from VA3D is like VR7 a different species of small-sized *Megacricetodon*.

Valdemoros 8A is the youngest locality of the local zone Db, which contains three species of *Megacricetodon* (*M. vandermeuleni*, *M. primitivus* and the first occurrence of *M. alvarezae* sp. nov.). In addition, Munébrega 3A should be considered the oldest locality of the zone Dc, since it contains *M. alvarezae* sp. nov. and the last occurrence of *M. primitivus*. Besides, Munébrega 3A and Vargas 5 are the samples of *M. alvarezae* sp. nov. having the largest dental dimensions, which suggests a decrease in size of *Megacricetodon* within this local zone.

The localities of Valdemoros 9 and Valdemoros 11 are magnetostratigraphically dated (Krijgsman et al., 1996; van Dam et al., 2006). These localities are correlated with Fuente Sierra 4 (assigned to local zone Db) and to the Vargas section. Valdemoros 9 is stratigraphically lower than Valdemoros 11, unfortunately the material of this site is very scarce. However, the material of *Megacricetodon* from the locality of Valdemoros 11 shows an intermediate size and morphology among the other population of *M. alvarezae* sp. nov., and allows to determine the intermediate position of this site.

The localities of Villafeliche 4A and Villafeliche 4B could be considered as the youngest sites of the local zone Dc, given that they contain the *M. alvarezae* sp. nov. of smaller size. Moreover, these localities contain three species of *Microdyromys*, *M. koenigswaldi*, M. *monspeliensis* and *M. remmerti* (García Paredes, 2006; García Paredes et al., 2009). The latter species have been recorded in Valdemoros 3B and Villafeliche 4A and 4B, being absent on the other Dc localities. On the contrary this faunal association is characteristics of the lower part of zone Dd, and therefore supports the younger age proposed for the Villafeliche 4 localities.

Finally, in disagreement to van der Meulen et al. (2012) we consider that the locality of Valdemoros 3D could be included in the local zone Dd, based on the *Megacricetodon* assemblage recorded in this locality. The *Megacricetodon* species of this site shows important differences with *M. alvarezae* sp. nov., both in size and morphology (smaller size and different morphology of the first lower molar) as will be discussed on the next chapter.

Of course these changes in the relative position of the localities of the local zone should be checked with the rest of the fauna of the biozone.

5.7. CONCLUSIONS

The study of the *Megacricetodon* material from the new and already known localities of the local zone Dc (MN5) from the Calatayud-Montalbán Basin, allow us to propose a new species of *Megacricetodon*, *M. alvarezae* sp. nov. This medium-sized species is characterized by having the m1 with well-individualized anteroconid with conical shaped and its low anterolophids that reaches only the base of the anteroconid).

Despite the larger size of *Megacricetodon alvarezae* sp. nov. compared to *M. primitivus*, we proposed a close relationship between this two species. *Megacricetodon alvarezae* sp. nov., a taxon so far only recorded on the Iberian Peninsula, might have migrated into Spain from Portugal at a period correlable to the end of the local zone Db, reaching its maximal distribution in the local zone Dc. The new species exhibits a slightly decrease in size throughout the biozone, but keeping its dental morphology unchanged.

5.8. REFERENCES

Aguilar, J. 1980a. Nouvelle interpretation de l'evolution du genre *Megacricetodon* au cours du Miocene. Paleovertebrata Volumen Jubilaire R. Lavocat:355-366.

Aguilar, J. P. 1981. Evolution des Rongeurs Miocenes et Paleogeographie de la Méditerranée occidentale. Université de Montpellier.

Aguilar, J. P. 1995. Evolution de la lignée *Megacricetodon collongensis-Megacricetodon rousillonensis* (Cricetidae, Rodentia, Mammalia) au cours du Miocène inférieur et moyen dans le sud de la France. Palaeovertebrata 24:1-45.

Aguilar, J. P., G. Clauzon, and J. Michaux. 1999. Nouveaux Cricétidés (Rodentia, Mammalia) dans le Miocène moyen de la région de Digne (Alpes de Haute Provence) Systématique, Biocronologie, Corrélations. Paleontographica, 253(1-3):1-28.

Alcalá, L., A. Alonso-Zarza, M. Álvarez-Sierra, B. Azanza, J. Calvo, J. Cañaveras, J. v. Dam, M. Garcés, W. Krijgsman, A. v. d. Meulen, P. Pélaez-Campomanes, Pérez-González.A, S. Sánchez Moral, R. Sancho, and E. Sanz Rubio. 2000. El registro sedimentario y faunístico de las cuencas de calatayud-daroca y teruel. evolución paleoambiental y paleoclimática durante el neógeno. Revista de la Sociedad Geológica de España 13:323-343.

Alvarez-Sierra, M. A., and E. García-Moreno. 1986. New Gliridae and Cricetidae from the Middle and Upper Miocene of the Duero Basin, Spain. Studia Geologica Salmanticensia 22:145-189.

Antunes, M. T. 2000. Miocene mammals from Lisbon and geologic age. A showcase for marine-continental correlations. Ciências da Terra (UNL) 14:343-348.

Antunes, M. T., P. Legoinha, A. Nascimento, and J. Pais. 1996. The evolution of the Lower Tagus basin (Lisbon and Setubal Peninsula, Portugal) from Lower to early Middle Miocene. Geologie de la France 4:59-77.

Antunes, M. T., and P. Mein. 1971. Notes sur la géologie et la paléontologie du Miocène de Lisbonne IX rongeurs et insectivores (Burdigalien Inférieur et Helvétien inférieur). Revista da Facultad de Ciencia Lisboa 16:327-349.

Bi, S., J. Meng, and W. Wu. 2008. A new species of *Megacricetodon* (Cricetidae, Rodentia, Mammalia) from the Middle Miocene of northern Junggar Basin, China. American Museum Novitates 3602:1-23.

Bowdich, T. E. 1821. An Analysis of the Natural Classification of Mamalia for the Use of Students and Travellers. 115 pp. Smith, J., Paris.

Bulot, C. 1980. Nouvelle description de deux especes du genre *Megacricetodon* (Cricetidae, Rodentia) du Miocene de Bezian (Zone de La Romieu). Bulletin du Museum National d'Histoire Naturelle Section C Sciences de la Terre Paleontologie Geologie Mineralogie 2:3-16.

Daams, R., L. Alcalá, M. A. Alvarez Sierra, B. Azanza, J. A. van Dam, A. J. van der Meulen, J. Morales, M. Nieto, P. Peláez-Campomanes, and D. Soria. 1998. A stratigraphical framework for Miocene (MN4-MN13) continental sediments of central Spain. Comptes Rendus de l'Academie des Sciences, Serie II. Sciences de la Terre et des Planetes 327:625-631.

Daams, R., and M. Freudenthal. 1988a. Cricetidae (Rodentia) from the type-Aragonian: the genus Megacricetodon; pp. 39-132 *i*n M. Freudenthal (ed.), Biostratigraphy and paleoecology of the Neogene micromammalian faunas from the Calatayud-Teruel Basin (Spain). Scripta Geologica, Special Issue 1, Leiden.

Daams, R., and M. Freudenthal. 1988b. Synopsis of the Dutch-Spanish collaboration program in the Neogene of the Calatayud-Teruel basin, p. 3-18. *In* M. Freudenthal (ed.), Biostratigraphy and paleoecology of the Neogene micromammalian faunas from the Calatayud-Teruel Basin (Spain). Scripta Geologica, Special Issue 1, Leiden.

Daams, R., A. J. van der Meulen, M. A. Álvarez-Sierra, P. Peláez-Campomanes, J. P. Calvo, M. A. Alonso Zarza, and W. Krijgsman. 1999a. Stratigraphy and sedimentology of the Aragonian (Early to Middle Miocene) in its type area (North-Central Spain). Newsletters on Stratigraphy 37:103-139.

Daams, R., A. J. van der Meulen, M. A. Álvarez-Sierra, P. Peláez-Campomanes, and W. Krijgsman. 1999b. Aragonian stratigraphy reconsidered, and a re-evaluation of the middle Miocene mammal biochronology in Europe. Earth and Planetary Science Letters 165:287-294.

Daxner, G. 1967. Ein neuer cricetodontide (Rodentia, Mammalia) aus dem Pannon des Wiener Beckens. Annalen des Naturhistorischen Museums in Wien 71:27-36.

Fahlbusch, V. 1964. Die Cricetiden (Mam.) der Oberen Süsswasser-Molasse Bayerns. Bayerische Akademie Wissenschaften. Mathematisch-naturwissenschaftliche Klasse. Munchen 118:1-135.

Freudenthal, M. 1963. Entwicklungsstufen der Miozänen Cricetodontinae (Mam. Rod.). In *Mittelspaniens und ihre Stratigraphische Bedeutung*, pp. 107. Ricks University, Utrecht.

García Paredes, I. 2006. Patrones evolutivos de los Gliridae (Rodentia, Mammalia) del Mioceno inferior y medio del área tipo del Aragoniense (Cuenca de Calatayud-Montalbán), Universidad Complutense de Madrid, Madrid, 676 p.

García-Paredes, I., P. Peláez-Campomanes, and M. A. Álvarez-Sierra. 2009. Gliridae (Rodentia, Mammalia) with a simple dental pattern: a new genus and new species from the European Early and Middle Miocene. Zoological Journal of the Linnean Society, 157(3):622-652.

Herráez, E., I. García Paredes, P. Peláez-Campomanes, and J. Morales. 2006. Los Nogales, nueva fauna de vertebrados del Mioceno medio de Madrid. Estudios Geológicos 62:257-262.

Illiger, J. K. W. 1811. Überblick der Säugthiere nach ihrer Vertheilung über die Welttheile.; pp. 39-160 *i*n W. d. Gruyter (ed.), Abhandlungen de physikalischen Klasse der Königlich-Preussischen Akademie der Wissenschaften. Realschul-Buchhandlung, Berlin.

Krijgsman, W., M. Garcés, C. G. Langereis, R. Daams, J. Vand Dam, A. J. van der Meulen, J. Aagustí, and L. Cabrera. 1996. A new chronology for the middle to late Miocene continental record in Spain. Earth and Planetary Science Letters, 142(3-4):367-380.

Lazzari, V., and J. P. Aguilar. 2007. Les *Megacricetodon* du gisement karstique miocène moyen de Blanquatère 1 (Pyrénées-Orientales, Sud de la France): nouvelles espèces, implications biochronologique et phylogénetique. Geobios 40:91-111.

Lindsay, E. H. 1988. Cricetid rodents from Siwalik deposits near Chinji Village: part 1: Megacricetodontinae, Myocridetontinae and Dendromurinae. Paleovertebrata 18:95-154.

Maridet, O. 2003. Révision du genre Democricetodon (Mammalia, Rodentia, Cricetinae) et dynamique des faunes de rongeurs du Néogène d'Europe occidentale : évolution, paléobiodiversité et paléobiogéographie, pp. 1-253. l'Universite Claude Bernard – Lyon 1, Lyon.

Maridet, O., W.-Y. Wu, J. Ye, S.-D. Bi, X.-J. Ni, and J. Meng. 2011. Early Miocene cricetids (Rodentia) from the Junggar basin (Xinjiang, China) and their biochronological implications. Geobios (Villeurbanne) 44.

Mein, P. 1958. Les mammifères de la faune sidérolithique du Vieux -Collonges. Nouvelles Archives du Muséum d'Histoire Naturelle de Lyon 5:1-122.

Oliver, A., and P. Pelaez-Campomanes. 2013. *Megacricetodon vandermeuleni*, sp. nov. (Rodentia, Mammalia), from the Spanish Miocene: a new evolutionary framework for *Megacricetodon*. Journal of Vertebrate Paleontology 33:943-955.

Oliver Pérez, A., P. López-guerrero, and P. Pelaez-Campomanes. 2008. Primer representante del género *Megacricetodon* de la Cuenca de Calatayud-Daroca (Zaragoza, España); pp. 317-329 *in* J. Esteve, and G. Meléndez (eds.), Palaeontológica Nova. Publicaciones del Seminario de Paleontología de Zaragoza, Zaragoza.

Peláez-Campomanes, P., and R. Daams. 2002. Middle Miocene rodents from Pasalar, Anatolia, Turkey. Acta Palaeontologica Polonica 47:125-132.

Qiu, Z., C. Li, and S. Wang. 1981. Miocene mammalian fossils from Xining Basin, Qinghai. Vertebrata Palasiatica 19:156-173.

Radulescu, C., and P. Samson. 1988. Les cricetides (Rodentia, Mammalia) du Miocene (Astaracien superieur) de Roumanie. Travaux de l'Institut de Speologie "Emile Racovitza" 27:67-78.

Schaub, S. 1925. Die Hamsterartige Nagetiere des Tertiärs und ihre lebenden Verwandten. Abhandlungen des Schweizerischen paläontologische Gesellschaft - Mémoires de la Société paléontologique suisse 45 (Années1921-25):1-114.

Sesé, C. 2006. Los roedores y lagomorfos del Neógeno de España. Estudios Geológicos 62:429-480.

van Dam, J. A., H. A. Aziz, M. A. A. Sierra, F. J. Hilgen, L. W. V. D. H. Ostende, L. J. Lourens, P. Mein, A. J. van der Meulen, and P. Pelaez-Campomanes. 2006. Long-period astronomical forcing of mammal turnover. Nature 443:687-691.

van der Meulen, A. J., and R. Daams. 1992. Evolution of Early-Middle Miocene rodent faunas in relation to long-term palaeoenvironment changes. Palaeogeography, Palaeoclimatology, Palaeoecology 93:227-253.

van der Meulen, A. J., I. Garcia-Paredes, M. A. Alvarez-Sierra, L. W. V. Ostende, K. Hordijk, A. Oliver, P. Lopez-Guerrero, V. Hernandez-Ballarin, and P. Pelaez-Campomanes. 2011. Biostratigraphy or biochronology? Lessons from the Early and Middle Miocene small Mammal Events in Europe. Geobios 44:309-321.

van der Meulen, A. J., I. García-Paredes, M. A. Álvarez-Sierra, L. W. van den Hoek Ostende, K. Hordijk, A. Oliver, and P. Peláez-Campomanes. 2012. Updated Aragonian biostratigraphy: Small Mammal distribution and its implications for the Miocene European Chronology. Geologica Acta 10:159-179.

APPENDIX 5.1

DISTRIBUTION OF CHARACTER STATES

Table 1. Anterocone M1

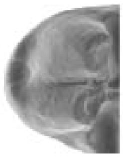
Localities						N
Villafeliche 4B		1 (7%)	1 (7%)	12 (80%)	1 (7%)	15
Villafeliche 4A		1 (2%)	9 (20%)	28 (64%)	6 (14%)	44
Valdemoros 3B	1 (3%)	3 (8%)	4 (11%)	26 (72%)	2 (6%)	36
Vargas 6		2 (7%)	3 (11%)	22 (81%)		27
Valdemoros 11			2 (25%)	5 (63%)	1 (13%)	8
Vargas 5		2 (10%)	5 (25%)	12 (60%)	1 (5%)	20
Valdemoros 9				1 (100%)		1
Munebrega 3A		1 (5%)	6 (32%)	12 (63%)		19

Table 2. Symmetry of the Anterocone M1

Localities			N
Villafeliche 4B	1 (6%)	17 (94%)	18
Villafeliche 4A	6 (11%)	51 (89%)	57
Valdemoros 3B	7 (16%)	36 (84%)	43
Vargas 6	3 (9%)	31 (91%)	34
Valdemoros 11	2 (17%)	10 (83%)	12
Vargas 5	2 (9%)	21 (91%)	23
Valdemoros 9		1 (100%)	1
Munebrega 3A		23 (100%)	23

Table 3. Anterolophule M1

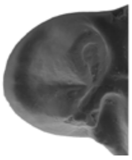
Localities				N
Villafeliche 4B	8 (44%)	10 (56%)		18
Villafeliche 4A	27 (44%)	33 (54%)	1 (2%)	61
Valdemoros 3B	14 (33%)	29 (67%)		43
Vargas 6	15 (42%)	19 (53%)	2 (6%)	36
Valdemoros 11	5 (38%)	7 (54%)	1 (8%)	13
Vargas 5	10 (43%)	10 (43%)	3 (13%)	23
Valdemoros 9		1 (100%)		1
Munebrega 3A	5 (24%)	16 (76%)		21

Table 4. Labial Spur of the Anterolophule M1

Localities				N
Villafeliche 4B	2 (11%)	1 (6%)	15 (83%)	18
Villafeliche 4A	15 (21%)	6 (9%)	49 (70%)	70
Valdemoros 3B	5 (12%)	2 (5%)	36 (84%)	43
Vargas 6	11 (25%)	3 (7%)	30 (68%)	44
Valdemoros 11	2 (14%)		12 (86%)	14
Vargas 5	10 (32%)	3 (10%)	18 (58%)	31
Valdemoros 9			1 (100%)	1
Munebrega 3A	1 (4%)	2 (8%)	21 (88%)	24

Table 5. Protolophule of the M1

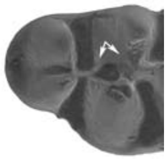
Localities				N
Villafeliche 4B	13 (72%)	3 (17%)	2 (11%)	18
Villafeliche 4A	52 (81%)	8 (13%)	4 (6%)	64
Valdemoros 3B	37 (88%)	2 (5%)	3 (7%)	42
Vargas 6	34 (83%)	5 (12%)	2 (5%)	41
Valdemoros 11	12 (86%)	1 (7%)	1 (7%)	14
Vargas 5	24 (80%)	3 (10%)	3 (10%)	30
Valdemoros 9	1 (100%)			1
Munebrega 3A	20 (95%)		1 (5%)	21

Table 6. Ectoloph M1

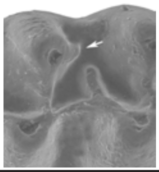
Localities				N
Villafeliche 4B	4 (24%)	13 (76%)		17
Villafeliche 4A	23 (35%)	43 (65%)		66
Valdemoros 3B	10 (23%)	33 (77%)		43
Vargas 6	10 (26%)	28 (74%)		38
Valdemoros 11	4 (29%)	10 (71%)		14
Vargas 5	13 (41%)	17 (53%)	2 (6%)	32
Valdemoros 9		1 (100%)		1
Munebrega 3A	3 (13%)	20 (87%)		23

Table 7. Mesoloph M1

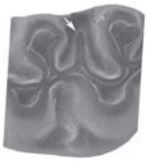
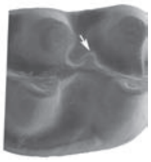
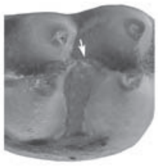
Localities					N
Villafeliche 4B		6 (33%)	12 (67%)		18
Villafeliche 4A	1 (1%)	16 (23%)	51 (74%)	1 (1%)	69
Valdemoros 3B	1 (2%)	14 (32%)	28 (64%)	1 (2%)	44
Vargas 6		12 (29%)	29 (71%)		41
Valdemoros 11		3 (20%)	12 (80%)		15
Vargas 5		18 (56%)	14 (44%)		32
Valdemoros 9			1 (100%)		1
Munebrega 3A		6 (26%)	17 (74%)		23

Table 8. Lingual mesocingulum of the M1.

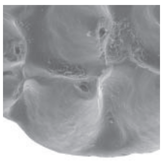
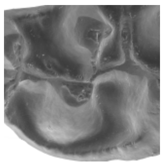
Localities			N
Villafeliche 4B	8 (44%)	10 (56%)	18
Villafeliche 4A	27 (39%)	42 (61%)	69
Valdemoros 3B	38 (88%)	5 (12%)	43
Vargas 6	28 (70%)	12 (30%)	40
Valdemoros 11	9 (75%)	3 (25%)	12
Vargas 5	27 (82%)	6 (18%)	33
Valdemoros 9		1 (100%)	1
Munebrega 3A	17 (68%)	8 (32%)	25

Table 9. Connection Mesoloph-Ectoloph M1

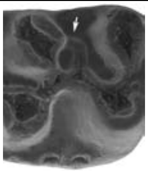
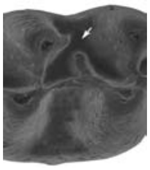
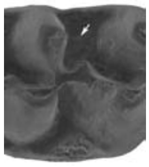
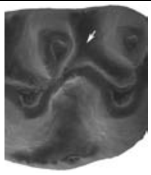
Localities					N
Villafeliche 4B	1 (6%)	12 (71%)	4 (24%)		17
Villafeliche 4A	2 (3%)	39 (61%)	22 (34%)	1 (2%)	64
Valdemoros 3B		32 (74%)	10 (23%)	1 (2%)	43
Vargas 6	1 (3%)	26 (68%)	11 (29%)		38
Valdemoros 11		9 (69%)	4 (31%)		13
Vargas 5	4 (13%)	15 (50%)	11 (37%)		30
Valdemoros 9		1 (100%)			1
Munebrega 3A		19 (90%)	2 (10%)		21

Table 10. Metalophule M1

Localities								N
Villafeliche 4B				14 (93%)	1 (7%)			15
Villafeliche 4A	1 (2%)	1 (2%)	4 (8%)	44 (83%)	2 (4%)		1 (2%)	53
Valdemoros 3B				39 (95%)	1 (2%)	1 (2%)		41
Vargas 6				28 (93%)	2 (7%)			30
Valdemoros 11		1 (8%)	1 (8%)	11 (85%)				13
Vargas 5			1 (4%)	23 (96%)				24
Valdemoros 9				1 (100%)				1
Munebrega 3A			3 (15%)	17 (85%)				20

Table 11. Protolophule M2

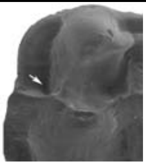
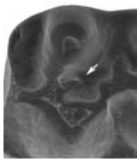
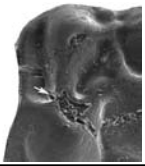
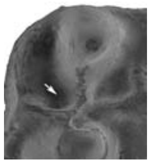
Localities						N
Villafeliche 4B	16 (89%)	1 (6%)	1 (6%)			18
Villafeliche 4A	32 (74%)	5 (12%)	1 (2%)	1 (2%)	4 (9%)	43
Valdemoros 3B	40 (78%)	4 (8%)	2 (4%)		5 (10%)	51
Vargas 6	26 (74%)	4 (11%)	4 (11%)		1 (3%)	35
Valdemoros 11	9 (56%)	1 (6%)	4 (25%)	1 (6%)	1 (6%)	16
Vargas 5	16 (76%)	3 (14%)			2 (10%)	21
Munebrega 3A	15 (65%)	7 (30%)	1 (4%)			23

Table 12. Anterior Protolophule M2

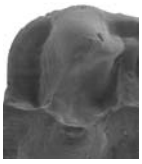
Localities			N
Villafeliche 4B	16 (94%)	1 (6%)	17
Villafeliche 4A	37 (100%)		37
Valdemoros 3B	43 (100%)	1 (2%)	44
Vargas 6	30 (100%)		30
Valdemoros 11	8 (80%)	2 (20%)	10
Vargas 5	15 (79%)	4 (21%)	19
Munebrega 3A	20 (91%)	2 (9%)	22

Table 13. Ectoloph M2

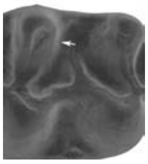
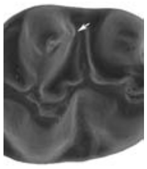
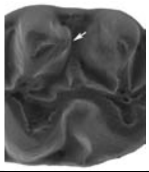
Localities				N
Villafeliche 4B	6 (29%)	15 (71%)		21
Villafeliche 4A	9 (17%)	35 (67%)	8 (15%)	52
Valdemoros 3B	10 (19%)	34 (63%)	10 (19%)	54
Vargas 6	7 (17%)	32 (78%)	2 (5%)	41
Valdemoros 11	2 (11%)	12 (67%)	4 (22%)	18
Vargas 5	4 (15%)	17 (65%)	5 (19%)	26
Munebrega 3A	1 (4%)	21 (78%)	5 (19%)	27

Table 14. Mesoloph M2

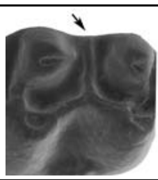
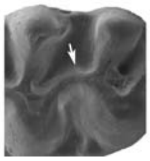
Localities					N
Villafeliche 4B		13 (54%)	11 (46%)		24
Villafeliche 4A		24 (44%)	29 (54%)	1 (2%)	54
Valdemoros 3B		26 (47%)	28 (51%)	1 (2%)	55
Vargas 6	1 (2%)	18 (43%)	23 (55%)		42
Valdemoros 11	1 (5%)	14 (74%)	4 (21%)		19
Vargas 5	1 (4%)	14 (54%)	11 (42%)		26
Munebrega 3A		10 (37%)	17 (63%)		27

Table 15. Connection Mesolph-Ectoloph M2

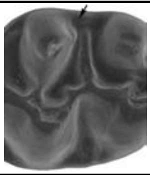
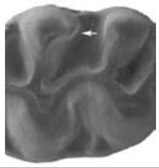
Localities					N
Villafeliche 4B	3 (15%)	11 (55%)	6 (30%)		20
Villafeliche 4A	6 (12%)	34 (69%)	8 (16%)	1 (2%)	49
Valdemoros 3B	6 (11%)	38 (70%)	10 (19%)		54
Vargas 6	2 (5%)	31 (78%)	7 (18%)		40
Valdemoros 11	3 (17%)	13 (72%)	2 (11%)		18
Vargas 5	10 (38%)	12 (46%)	4 (15%)		26
Munebrega 3A	8 (30%)	18 (67%)	1 (4%)		27

Table 16. Metalophule M2

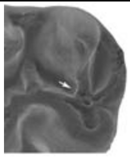
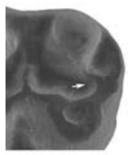
Localities								N
Villafeliche 4B	11 (61%)	1 (6%)	1 (6%)	4 (22%)			1 (6%)	18
Villafeliche 4A	24 (62%)	2 (5%)		9 (23%)			4 (10%)	39
Valdemoros 3B	34 (65%)		1 (2%)	15 (29%)	2 (4%)			52
Vargas 6	25 (76%)		2 (6%)	4 (12%)	1 (3%)		1 (3%)	33
Valdemoros 11	9 (56%)	1 (6%)	1 (6%)	3 (19%)			2 (13%)	16
Vargas 5	18 (82%)		1 (5%)	2 (9%)		1 (5%)		22
Munebrega 3A	17 (74%)		3 (13%)	3 (13%)				23

Table 17. Metalophule M3

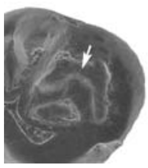
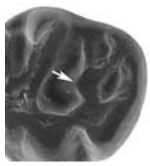
Localities						N
Villafeliche 4B		2 (50%)	1 (25%)		1 (25%)	4
Villafeliche 4A	1 (33%)	1 (33%)	1 (33%)			3
Valdemoros 3B	8 (40%)	3 (15%)	5 (25%)	2 (10%)	2 (10%)	20
Vargas 6		6 (67%)	1 (11%)		2 (22%)	9
Valdemoros 11		1 (100%)				1
Vargas 5	1 (25%)		1 (25%)		2 (50%)	4
Valdemoros 9			1 (100%)			1
Munebrega 3A	3 (50%)		2 (33%)		1 (17%)	6

Table 18. Anteroconid m1

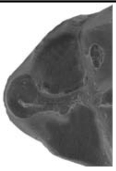
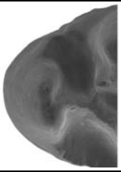
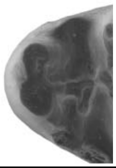
Localities				N
Villafeliche 4B	14 (67%)	5 (24%)	2 (10%)	21
Villafeliche 4A	32 (52%)	24 (39%)	6 (10%)	62
Valdemoros 3B	22 (63%)	10 (29%)	3 (9%)	35
Vargas 6	18 (60%)	8 (27%)	4 (13%)	30
Valdemoros 11	3 (50%)	3 (50%)		6
Vargas 5	13 (76%)	2 (12%)	2 (12%)	17
Valdemoros 9	2 (100%)			2
Munebrega 3A	18 (78%)	5 (22%)		23

Table 19. Labial Spur of the Anterolophulid m1

Localities				N
Villafeliche 4B	16 (76%)		5 (24%)	21
Villafeliche 4A	56 (79%)	5 (7%)	10 (14%)	71
Valdemoros 3B	30 (79%)	3 (8%)	5 (13%)	38
Vargas 6	25 (68%)	3 (8%)	9 (24%)	37
Valdemoros 11	5 (63%)	1 (13%)	2 (25%)	8
Vargas 5	15 (71%)		6 (29%)	21
Valdemoros 9	2 (100%)			2
Munebrega 3A	11 (39%)	4 (14%)	13 (46%)	28

Table 20. Metalophulid m1

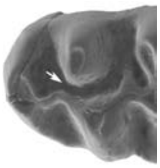
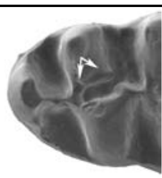
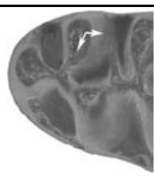
Localities					N
Villafeliche 4B		17 (85%)	1 (5%)	2 (10%)	20
Villafeliche 4A	2 (2%)	60 (86%)	5 (7%)	3 (4%)	70
Valdemoros 3B		35 (97%)	1 (3%)		36
Vargas 6	2 (3%)	32 (89%)	2 (6%)		36
Valdemoros 11		8 (89%)		1 (11%)	9
Vargas 5		9 (41%)	7 (32%)	6 (27%)	22
Valdemoros 9		2 (100%)			2
Munebrega 3A		20 (83%)	1 (4%)	3 (13%)	24

Table 21. Mesolophid m1

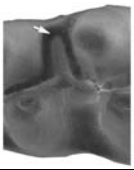
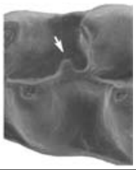
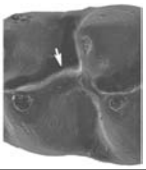
Localities				N
Villafeliche 4B	1 (5%)	17 (85%)	2 (10%)	20
Villafeliche 4A	1 (1%)	57 (72%)	21 (27%)	79
Valdemoros 3B		23 (66%)	12 (34%)	35
Vargas 6	3 (9%)	28 (80%)	4 (11%)	35
Valdemoros 11	1 (9%)	9 (82%)	1 (9%)	11
Vargas 5	1 (4%)	22 (88%)	2 (8%)	25
Valdemoros 9		2 (100%)		2
Munebrega 3A	1 (4%)	24 (96%)		25

Table 22. Ectomesolophid m1

Localities		N
Villafeliche 4B	22 (100%)	22
Villafeliche 4A	87 (100%)	87
Valdemoros 3B	38 (100%)	38
Vargas 6	35 (100%)	35
Valdemoros 11	11 (100%)	11
Vargas 5	25 (100%)	25
Valdemoros 9	3 (100%)	3
Munebrega 3A	24 (100%)	24

Table 23. Lingual Anterolophid m2

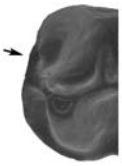
Localities				N
Villafeliche 4B	1 (10%)	6 (60%)	3 (30%)	10
Villafeliche 4A	14 (24%)	35 (60%)	9 (16%)	58
Valdemoros 3B	1 (3%)	28 (70%)	11 (28%)	40
Vargas 6	2 (5%)	33 (80%)	6 (15%)	41
Valdemoros 11	1 (17%)	4 (67%)	1 (17%)	6
Vargas 5	3 (12%)	20 (77%)	3 (12%)	26
Valdemoros 9		1 (100%)		1
Munebrega 3A	3 (17%)	14 (78%)	1 (6%)	18

Table 24. Mesolophid m2

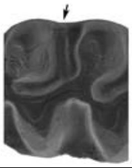
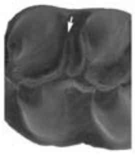
Localities				N
Villafeliche 4B		11 (92%)	1 (8%)	12
Villafeliche 4A		55 (80%)	14 (20%)	69
Valdemoros 3B	1 (2%)	33 (65%)	17 (33%)	51
Vargas 6	1 (2%)	40 (87%)	5 (11%)	46
Valdemoros 11		8 (100%)		8
Vargas 5		29 (85%)	5 (15%)	34
Valdemoros 9		1 (100%)		1
Munebrega 3A		25 (100%)		25

Table 25. Lingual Anterolophid m3

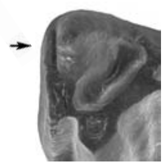
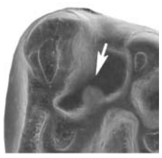
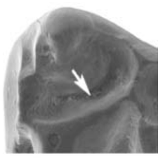
Localities				N
Villafeliche 4B			3 (100%)	3
Villafeliche 4A		4 (100%)		4
Valdemoros 3B	2 (8%)	15 (63%)	7 (29%)	24
Vargas 6		8 (89%)	1 (11%)	9
Valdemoros 11		2 (67%)	1 (33%)	3
Vargas 5		5 (100%)		5
Munebrega 3A	3 (30%)	6 (60%)	1 (10%)	10

Table 26. Mesolophid m3

Localities				N
Valdemoros 8A	(*M. vandermeuleni*)	1 (8%)	12 (92%)	13
Moratilla 2	(*M. vandermeuleni*)	2 (11%)	17 (89%)	19
Fuente Sierra 4	(*M. vandermeuleni*)		3 (100%)	3
La Retama	(*M. vandermeuleni*)		2 (100%)	2
La Col-D	(*M. vandermeuleni*)		3 (100%)	3
Villafeliche 4B			4 (100%)	4
Villafeliche 4A			5 (100%)	5
Valdemoros 3B			30 (100%)	30
Vargas 6			12 (100%)	12
Valdemoros 11			4 (100%)	4
Vargas 5			4 (100%)	4
Munebrega 3A			12 (100%)	12

APPENDIX 5.2

Table 1. Levene's test of the lower and upper molars of *Megacricetodon alvarezae* sp. nov. All analyses were accomplished using exclusively localities with sample sizes larger than four specimens.

		Levene's test	gl1	gl2	Significance
m1	Length (mm)	1,175	5	105	0,326
	Width (mm)	2,301	5	144	0,048
m2	Length (mm)	1,31	5	123	0,264
	Width (mm)	2,834	5	134	0,018
M1	Length (mm)	0,391	5	99	0,854
	Width (mm)	1,003	5	131	0,419
M2	Length (mm)	0,619	5	129	0,685
	Width (mm)	0,283	5	128	0,922

Table 2. Post hoc of the lower first molars of *Megacricetodon alvarezae* sp. nov. using localities with sample sizes larger than four specimens. For the length t, we carried out Hochberg's GT2 due to the equal variances assumed; and for the width we carried out Games-Howell because of the different variances assumed.

		Localities	Localities	Mean Difference	Standard error	Significance
LENGHT m1	Hochberg	MUN3A	VA11	0,0649	0,02906	0,335
			VR5	-0,007	0,02118	1,000
			VR6	0,0582	0,02038	0,074
			VL4A	0,0831	0,01637	0,000
			VL4B	0,0976	0,02075	0,000
		VA11	MUN3A	-0,0649	0,02906	0,335
			VR5	-0,0718	0,02984	0,231
			VR6	-0,0067	0,02929	1,000
			VL4A	0,0183	0,02665	1,000
			VL4B	0,0327	0,02955	0,989
		VR5	MUN3A	0,007	0,02118	1,000
			VA11	0,0718	0,02984	0,231
			VR6	0,0652	0,02149	0,044
			VL4A	0,0901	0,01773	0,000
			VL4B	0,1046	0,02184	0,000
		VR6	MUN3A	-0,0582	0,02038	0,074
			VA11	0,0067	0,02929	1,000
			VR5	-0,0652	0,02149	0,044
			VL4A	0,0249	0,01678	0,886
			VL4B	0,0394	0,02108	0,617
		VL4A	MUN3A	-0,0831	0,01637	0,000
			VA11	-0,0183	0,02665	1,000
			VR5	-0,0901	0,01773	0,000
			VR6	-0,0249	0,01678	0,886
			VL4B	0,0145	0,01723	0,999
		VL4B	MUN3A	-0,0976	0,02075	0,000
			VA11	-0,0327	0,02955	0,989
			VR5	-0,1046	0,02184	0,000
			VR6	-0,0394	0,02108	0,617
			VL4A	-0,0145	0,01723	0,999
WIDTH m1	Games-Howell	MUN3A	VA11	0,047	0,01801	0,145
			VR5	0,0082	0,01383	0,991
			VR6	0,0423	0,01404	0,053
			VL4A	0,0566	0,01336	0,003
			VL4B	0,0645	0,01526	0,002
		VA11	MUN3A	-0,047	0,01801	0,145
			VR5	-0,0388	0,0141	0,161
			VR6	-0,0047	0,01431	0,999
			VL4A	0,0096	0,01364	0,976
			VL4B	0,0175	0,01551	0,861
		VR5	MUN3A	-0,0082	0,01383	0,991
			VA11	0,0388	0,0141	0,161
			VR6	0,034	0,00846	0,003
			VL4A	0,0484	0,00728	0,000
			VL4B	0,0563	0,01036	0,000
		VR6	MUN3A	-0,0423	0,01404	0,053
			VA11	0,0047	0,01431	0,999
			VR5	-0,034	0,00846	0,003
			VL4A	0,0143	0,00767	0,435
			VL4B	0,0222	0,01064	0,319
		VL4A	MUN3A	-0,0566	0,01336	0,003
			VA11	-0,0096	0,01364	0,976
			VR5	-0,0484	0,00728	0,000
			VR6	-0,0143	0,00767	0,435
			VL4B	0,0079	0,00972	0,963
		VL4B	MUN3A	-0,0645	0,01526	0,002
			VA11	-0,0175	0,01551	0,861
			VR5	-0,0563	0,01036	0,000
			VR6	-0,0222	0,01064	0,319
			VL4A	-0,0079	0,00972	0,963

Table 3. Post hoc of the lower second molars of *Megacricetodon alvarezae* sp. nov. using localities with sample sizes larger than four specimens. Both for the length t and width of the m2, we carried out Hochberg's GT2 due to the equal variances assumed.

		Localities	Localities	Mean Difference	Standard error	Significance
LENGTH m2	Hochberg	MUN3A	VA11	0,0291	0,01737	0,768
			VR5	-0,0056	0,01349	1,000
			VR6	0,0369	0,01259	0,058
			VL4A	0,0677	0,01139	0,000
			VL4B	0,0702	0,01665	0,001
		VA11	MUN3A	-0,0291	0,01737	0,768
			VR5	-0,0348	0,0165	0,425
			VR6	0,0078	0,01578	1,000
			VL4A	0,0386	0,01484	0,144
			VL4B	0,0411	0,01918	0,398
		VR5	MUN3A	0,0056	0,01349	1,000
			VA11	0,0348	0,0165	0,425
			VR6	0,0426	0,01136	0,004
			VL4A	0,0733	0,01002	0,000
			VL4B	0,0758	0,01574	0,000
		VR6	MUN3A	-0,0369	0,01259	0,058
			VA11	-0,0078	0,01578	1,000
			VR5	-0,0426	0,01136	0,004
			VL4A	0,0308	0,00877	0,009
			VL4B	0,0333	0,01498	0,341
		VL4A	MUN3A	-0,0677	0,01139	0,000
			VA11	-0,0386	0,01484	0,144
			VR5	-0,0733	0,01002	0,000
			VR6	-0,0308	0,00877	0,009
			VL4B	0,0025	0,01399	1,000
		VL4B	MUN3A	-0,0702	0,01665	0,001
			VA11	-0,0411	0,01918	0,398
			VR5	-0,0758	0,01574	0,000
			VR6	-0,0333	0,01498	0,341
			VL4A	-0,0025	0,01399	1,000
WIDHT m2	Hochberg	MUN3A	VA11	0,0529	0,01694	0,032
			VR5	0,0091	0,01217	1,000
			VR6	0,0489	0,01179	0,001
			VL4A	0,0727	0,01054	0,000
			VL4B	0,0688	0,01619	0,001
		VA11	MUN3A	-0,0529	0,01694	0,032
			VR5	-0,0437	0,01614	0,107
			VR6	-0,004	0,01585	1,000
			VL4A	0,0199	0,01494	0,949
			VL4B	0,0159	0,01935	1,000
		VR5	MUN3A	-0,0091	0,01217	1,000
			VA11	0,0437	0,01614	0,107
			VR6	0,0398	0,01061	0,004
			VL4A	0,0636	0,00919	0,000
			VL4B	0,0596	0,01534	0,002
		VR6	MUN3A	-0,0489	0,01179	0,001
			VA11	0,004	0,01585	1,000
			VR5	-0,0398	0,01061	0,004
			VL4A	0,0238	0,00869	0,098
			VL4B	0,0199	0,01505	0,952
		VL4A	MUN3A	-0,0727	0,01054	0,000
			VA11	-0,0199	0,01494	0,949
			VR5	-0,0636	0,00919	0,000
			VR6	-0,0238	0,00869	0,098
			VL4B	-0,004	0,01408	1,000
		VL4B	MUN3A	-0,0688	0,01619	0,001
			VA11	-0,0159	0,01935	1,000
			VR5	-0,0596	0,01534	0,002
			VR6	-0,0199	0,01505	0,952
			VL4A	0,004	0,01408	1,000

Table 4. Post hoc of the upper first molars of *Megacricetodon alvarezae* sp. nov. using localities with sample sizes larger than four specimens. Both for the length t and width of the M1, we carried out Tukey due to the equal variances assumed.

		Localities	Localities	Mean Difference	Standard error	Significance
LENGTH M1	Tukey	MUN3A	VA11	0,0852	0,02769	0,031
			VR5	0,0361	0,02281	0,613
			VR6	0,1149	0,02099	0,000
			VL4A	0,0954	0,01828	0,000
			VL4B	0,098	0,02236	0,000
		VA11	MUN3A	-0,0852	0,02769	0,031
			VR5	-0,0491	0,02864	0,525
			VR6	0,0297	0,02721	0,884
			VL4A	0,0102	0,02518	0,999
			VL4B	0,0129	0,02828	0,997
		VR5	MUN3A	-0,0361	0,02281	0,613
			VA11	0,0491	0,02864	0,525
			VR6	0,0788	0,02224	0,008
			VL4A	0,0593	0,0197	0,038
			VL4B	0,062	0,02353	0,099
		VR6	MUN3A	-0,1149	0,02099	0,000
			VA11	-0,0297	0,02721	0,884
			VR5	-0,0788	0,02224	0,008
			VL4A	-0,0195	0,01756	0,876
			VL4B	-0,0168	0,02177	0,971
		VL4A	MUN3A	-0,0954	0,01828	0,000
			VA11	-0,0102	0,02518	0,999
			VR5	-0,0593	0,0197	0,038
			VR6	0,0195	0,01756	0,876
			VL4B	0,0027	0,01917	1,000
		VL4B	MUN3A	-0,098	0,02236	0,000
			VA11	-0,0129	0,02828	0,997
			VR5	-0,062	0,02353	0,099
			VR6	0,0168	0,02177	0,971
			VL4A	-0,0027	0,01917	1,000
WIDHT M1	Tukey	MUN3A	VA11	0,0461	0,01946	0,175
			VR5	0,0275	0,01471	0,424
			VR6	0,0641	0,01365	0,000
			VL4A	0,0754	0,01277	0,000
			VL4B	0,0761	0,01601	0,000
		VA11	MUN3A	-0,0461	0,01946	0,175
			VR5	-0,0186	0,01902	0,925
			VR6	0,018	0,01822	0,921
			VL4A	0,0293	0,01757	0,554
			VL4B	0,03	0,02005	0,667
		VR5	MUN3A	-0,0275	0,01471	0,424
			VA11	0,0186	0,01902	0,925
			VR6	0,0366	0,01303	0,063
			VL4A	0,0479	0,0121	0,002
			VL4B	0,0486	0,01548	0,025
		VR6	MUN3A	-0,0641	0,01365	0,000
			VA11	-0,018	0,01822	0,921
			VR5	-0,0366	0,01303	0,063
			VL4A	0,0113	0,01079	0,900
			VL4B	0,012	0,01448	0,962
		VL4A	MUN3A	-0,0754	0,01277	0,000
			VA11	-0,0293	0,01757	0,554
			VR5	-0,0479	0,0121	0,002
			VR6	-0,0113	0,01079	0,900
			VL4B	0,0007	0,01365	1,000
		VL4B	MUN3A	-0,0761	0,01601	0,000
			VA11	-0,03	0,02005	0,667
			VR5	-0,0486	0,01548	0,025
			VR6	-0,012	0,01448	0,962
			VL4A	-0,0007	0,01365	1,000

Table 5. Post hoc of the upper second molars of *Megacricetodon alvarezae* sp. nov. using localities with sample sizes larger than four specimens. Both for the length t and width of the M2, we carried out Tukey due to the equal variances assumed.

		Localities	Localities	Mean Difference	Standard error	Significance
LENGTH M2	Tukey	MUN3A	VA11	0,0672	0,01703	0,002
			VR5	0,0289	0,01539	0,421
			VR6	0,0607	0,01387	0,000
			VL4A	0,0959	0,01253	0,000
			VL4B	0,0937	0,01593	0,000
		VA11	MUN3A	-0,0672	0,01703	0,002
			VR5	-0,0383	0,01758	0,256
			VR6	-0,0065	0,01628	0,999
			VL4A	0,0287	0,01515	0,410
			VL4B	0,0265	0,01806	0,686
		VR5	MUN3A	-0,0289	0,01539	0,421
			VA11	0,0383	0,01758	0,256
			VR6	0,0318	0,01455	0,251
			VL4A	0,067	0,01328	0,000
			VL4B	0,0648	0,01652	0,002
		VR6	MUN3A	-0,0607	0,01387	0,000
			VA11	0,0065	0,01628	0,999
			VR5	-0,0318	0,01455	0,251
			VL4A	0,0352	0,01149	0,031
			VL4B	0,033	0,01512	0,254
		VL4A	MUN3A	-0,0959	0,01253	0,000
			VA11	-0,0287	0,01515	0,410
			VR5	-0,067	0,01328	0,000
			VR6	-0,0352	0,01149	0,031
			VL4B	-0,0022	0,01391	1,000
		VL4B	MUN3A	-0,0937	0,01593	0,000
			VA11	-0,0265	0,01806	0,686
			VR5	-0,0648	0,01652	0,002
			VR6	-0,033	0,01512	0,254
			VL4A	0,0022	0,01391	1,000
WIDHT m2	Tukey	MUN3A	VA11	0,0564	0,01544	0,005
			VR5	0,0148	0,0137	0,890
			VR6	0,0523	0,01252	0,001
			VL4A	0,0692	0,01132	0,000
			VL4B	0,0881	0,01506	0,000
		VA11	MUN3A	-0,0564	0,01544	0,005
			VR5	-0,0417	0,0159	0,100
			VR6	-0,0041	0,01489	1,000
			VL4A	0,0128	0,01389	0,940
			VL4B	0,0317	0,01708	0,435
		VR5	MUN3A	-0,0148	0,0137	0,890
			VA11	0,0417	0,0159	0,100
			VR6	0,0376	0,01308	0,053
			VL4A	0,0545	0,01194	0,000
			VL4B	0,0733	0,01553	0,000
		VR6	MUN3A	-0,0523	0,01252	0,001
			VA11	0,0041	0,01489	1,000
			VR5	-0,0376	0,01308	0,053
			VL4A	0,0169	0,01055	0,599
			VL4B	0,0358	0,01449	0,141
		VL4A	MUN3A	-0,0692	0,01132	0,000
			VA11	-0,0128	0,01389	0,940
			VR5	-0,0545	0,01194	0,000
			VR6	-0,0169	0,01055	0,599
			VL4B	0,0189	0,01347	0,727
		VL4B	MUN3A	-0,0881	0,01506	0,000
			VA11	-0,0317	0,01708	0,435
			VR5	-0,0733	0,01553	0,000
			VR6	-0,0358	0,01449	0,141
			VL4A	-0,0189	0,01347	0,727

6. The lineage
M. collongensis - M. gersii

6.1. INTRODUCTION

As we discussed in the previous chapter, the middle Miocene material of *Megacricetodon* from the Calatayud-Montalbán Basin has been always assigned to *M. collongensis* (Daams & Freudenthal, 1988a, b; Daams et al., 1999). Van der Meulen et al. (2012), based on new studies and material, assigned the material from the local zone Dc to *Megacricetodon* n. sp. 2 maintaining as *M. collongensis* the material from the local zone Dd and E (Table 5.1). Based on the results of this work we consider that the first species, which occurs in the local zone Dc, is *Megacricetodon alvarezae* (Chapter 5), and that the *Megacricetodon* material from zones Dd and E should be assigned to two different species.

The species *Megacricetodon collongensis* was described by Mein in 1958, based on material from the French locality of Vieux-Collonges (near the city of Lyon). He described two new *Megacricetodon* species from this karstic locality (*M. collongensis* and *M. lappi*). Afterward, Freudenthal (1963) revised the material of *M. collongensis* from Vieux-Collonges and described in detail the type collection. Maridet (2003), in his thesis, study the cricetids of Vieux-Collonges, redefining the *Megacricetodon* species, and including a large amount of new material.

The material of *Megacricetodon collongensis* from Vieux-Collonges is a complicated and controversial population due to its high variability (in size and dental morphology; see Mein, 1958:86, and Maridet, 2003:116, table 55). Vieux-Collonges locality shows a strange association of mammal species, indicating a mixture of different faunas (see Maridet, 2003 for the complete fauna list). The karstic origin of this fossil accumulation might be the reason for this time averaging and the consequent extremely high morphometric variation of the *Megacricetodon* representatives.

As we previously discussed, every *Megacricetodon* forms showing a rather primitive morphology and with intermediate size from middle Miocene age were assigned to *M. collongensis*. In this way, Aguilar (1980), studying the karstic sediments of Languedoc-Roussillon, assigned the *Megacricetodon* from Port-la-Nouvelle to *M. collongensis*. According to him, *M. collongensis* from Port-la-Nouvelle shows the same morphological features as *M. collongensis* from Vieux-Collonges but with a larger dental size, and therefore, he considered the *Megacricetodon* from this locality would be younger than *Megacricetodon* from Vieux-Collonges. Afterwards Aguilar et al., (1986) assigned the *Megacricetodon* from the locality of Lo Fournas 1 (eastern Pyrenees, France) to *M. collongensis*. They considered that this assemblage was similar to *M. collongensis* from Port-la-Nouvelle.

However, subsequent studies began to differentiate *Megacricetodon* forms. Maridet (2003), revised the *Megacricetodon* material from Vieux-Collonges, and noted significant morphological differences between *M. collongensis* from Vieux-Collonges and *M. collongensis* from Port-la-Nouvelle and Lo Fournas 1. Lazzari & Aguilar (2007) in their work about the karstic locality of Blanquatère 1 (southern France), pointed out differences (both size and morphology) between *Megacricetodon collongensis* from Vieux-Collonges and "*M. collongensis*" from Port-la-Nouvelle, assigning to "*M. collongensis*" the material from the Languedoc-Roussillon sites until carried out a deeper review. Besides, they proposed a new *Megacricetodon* lineage that includes *M. tautavelensis*, a new small species proposed in this locality, *M. collongensis* from Vieux-Collonges and the small *M. rafaeli* from Spanish localities.

In the Iberian Peninsula, Hernández-Ballarín et al. (2010; 2011), studied the *Megacricetodon* from the Madrid Basin, correlated to biozone E, and they assigned the material to *Megacricetodon "collongensis"* and to *Megacricetodon "collongensis-gersii"*.

In this chapter, we will study and describe the *Megacricetodon* representatives from the middle Miocene of the Calatayud-Montalbán Basin focusing on the *Megacricetodon* forms from biozone Dd and E.

Objectives of the chapter:

- Describe and characterize the *Megacricetodon* species from the local zone Dd and E (middle Aragonian, middle Miocene).
- Propose a phylogenetic framework for these species.
- Propose a biochronological framework for this lineage in Europe.

6.2. MATERIAL

For the characterization of these *Megacricetodon* species, we have included 37 localities from the Calatayud-Montalbán Basin: Valdemoros 3D, Vargas 7, Vargas 8B, Vargas 8C, Valdemoros 8C, Valdemoros 8B, Valdemoros 7A, Valdemoros 7B, Valdemoros 7C, Valdemoros 3F, Las Umbrias 1, Las Umbrias 2, Vargas 11, Las Umbrias 3, Valdemoros 7D, Las Umbrias 4, Las Umbrias 5, Valdemoros 7F, Valdemoros 7G, Las Umbrias 7, Las Umbrias 8, Las Umbrias 9, Las Umbrias 10, Las Umbrias 11, Las Umbrias 12, Las Umbrias 14, Las Planas 4BA, Las Umbrias 16, Las Umbrias 17, Las Umbrias 18, Las Umbrias 19 and Las Umbrias20 are stored at the Museo Nacional de Ciencias Naturales, CSIC (Madrid, Spain). Casetón 1A, Casetón 2B, Valdemoros 3E are stored in the Nationaal Natuurhistorisch Museum-Naturalis (Leiden, The Netherlands). And Valdemoros 1A is stored at the Faculty of Earth Sciences in the University of Utrecht (Utrecht, The Netherlands).

In addition, we use the *Megacricetodon* data from the localities of Las Planas 4A, Las Planas 4B and Las Plans 4C published by Daams & Freudenthal (1988a).

Moreover, both in the tables of measurements and in the tables of the character states are included the data from *Megacricetodon gersii* from Sansan.

6.3. MORPHOMETRICAL RESULTS AND DISCUSSION

The metrical and morphological results are in the Tables 6.1-6.5 and in the Appendix 6.1 respectively.

The study of the tables of the descriptive statistics of the size, as well as the tables of distribution of character states show differences between the *Megacricetodon* assemblages from the lower part of the local zone Dd, and the assemblages from the upper part of the Dd and E. All the *Megacricetodon* material from the lowermost part of local zone Dd shows the same size and morphology through time (Appendix 6.1 and Tables 6.1-6.5). These lower associations are smaller in dental size than the *Megacricetodon* material from localities of the upper part of the local zone Dd and zone E. The latter *Megacricetodon* samples also show little changes (in dimensions and morphology) through time. In addition to those metric differences, the *Megacricetodon* assemblages from the lower part of the local zone Dd, differs morphologically from the *Megacricetodon* assemblages of the upper part by having the M1 with lower percentage of cingulum ridge in front of the anterocone, higher percentage of labial cusp smaller than the lingual one, longer mesoloph, lower percentage of ectoloph connected with the mesoloph; M2 with double ectoloph; m1 with higher percentage of simple anteroconid; and m2 with longer lingual anterolophid (see Tables 6.1-6.5 for differences in size and Appendix 6.1 for differences in morphology). The differences in size and morphology appears from the *Megacricetodon* material from the localities of Las Umbrias 1 (the last locality with the small *Megacricetodon*) and Las Umbrias 2 (the first locality with the larger *Megacricetodon*). The change in the *Megacricetodon* species coincides with a sedimentological change. The Valdemoros-Vargas Unit is overlaid by Las Umbrias Unit. The alternation of limestones and marls which form the upper part of the Valdemoros-Vargas Unit are overlaid by a succession of carbonates and marls included in Las Umbrias Unit. This change of units is interpreted as a distal part of alluvial fans with shallow carbonated lakes (Valdemoros-Vargas Unit) which evolved to a paludal environment with shallow lakes and marshes which underwent episodic subaerial exposure (Daams et al., 1999; Alcalá et al., 2000).

Based on all these results we agree with previous authors (Daams et al., 1999; van der Meulen et al., 2012) that the *Megacricetodon* assemblages of the local zones Dd and E represent successive representatives of a single lineage. Nevertheless, the observed differences within this lineage support, in our opinion, the differentiation of two successive species within the lineage. In this way, we propose the assignation to *Megacricetodon collongensis* the assemblages of the lower part of the biozone Dd (until Las Umbrias 1) and to *M. gersii* the material of the upper part of local zone Dd and E (from Las Umbrias 2) as will be discussed in the next section.

6.4. SYSTEMATIC PALAEONTOLOGY

Order RODENTIA Bowdich, 1821

Family MURIDAE Illiger, 1811

Subfamily CRICETODONTINAE Schaub, 1925

Genre *Megacricetodon* Fahlbusch, 1964

Megacricetodon collongensis (Mein, 1958)

(Figs. 6.1: 1-53)

Cricetodon minor primitivus from Valdemoros 1A in Freudenthal, 1963: 26-27.

Megacricetodon minor primitivus from Valdemoros 1A in Daams & Freudenthal, 1974: 5, 15.

Megacricetodon minor primitivus from Valdemoros 1A in Daams et al., 1977: 48, 52, fig. 3, 4, 5.

Megacricetodon primitivus from Valdemoros 1A in Freudenthal & Cuenca Bescos, 1984.

Megacricetodon primitivus from Valdemoros 1A in Daams & Freudenthal, 1988b: 14, fig. 8.

Holotype: Mandible m1-m3 left, Vx-C-386.

Type Locality: Vieux-Collonges, France.

Stratigraphical distribution: lower part of local zone Dd, middle Aragonian, middle Miocene.

Geographical distribution: Spain and France.

Measurements: Tables 6.1-6.5.

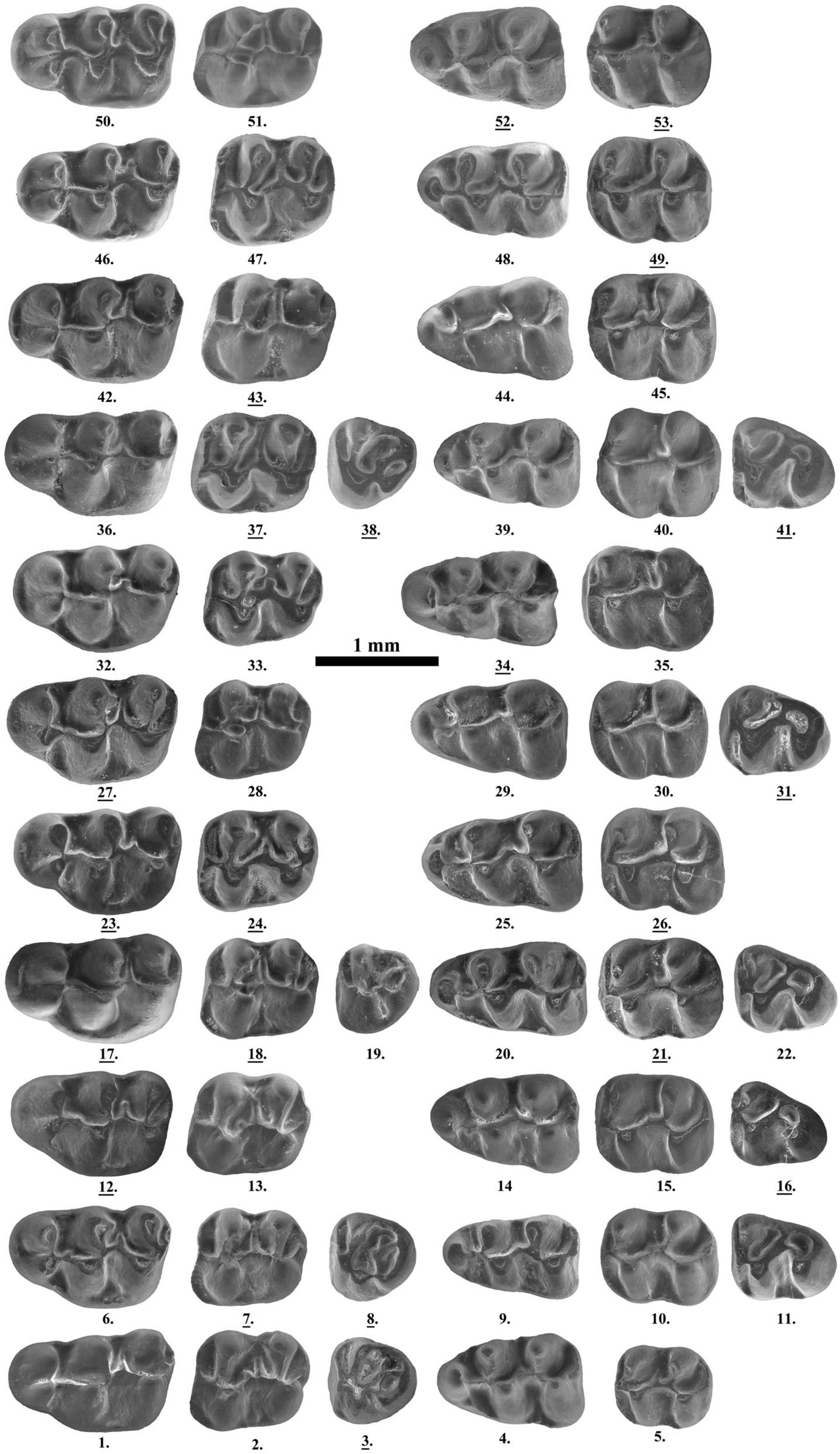


Figure 6.1. *Megacricetodon collongensis* from the Calatayud-Montalbán Basin. From Valdemoros 3D: 1, M1 VA3D-252.156; 2, M2 VA3D-265.747; 3, M3 VA3D-265.775; 4, m1 VA3D-265.792; 5, m2 VA3D-265.839. From Vargas 7: 6, M1 VR7-1126; 7, M2 VR7-1281; 8, M3 VR7-1304; 9, m1 VR7-1351; 10, m2 VR7-1426; 11, m3 VR7-1487. From Vargas 8B: 12, M1 VR8B-305; 13, M2 VR8B-330; 14, m1 VR8B-406; 15, m2 VR8B-455; 16, m3 VR8B-490. From Vargas 8C: 17, M1 VR8C-166; 18, M2 VR8C-251; 19, M3 VR8C-497; 20, m1 VR8C-269; 21, m2 VR8C-308; 22, m3 VR8C-483. From Valdemoros 8C: 23, M1 VA8C-103; 24, M2 VA8C-112; 25, m1 VA8C-119; 26, m2 VA8C-129. From Valdemoros 8B: 27, M1 VA8B-204; 28, M2 VA8B-208; 29, m1 VA8B-215; 30, m2 VA8B-219; 31, m3 VA8B-222. From Valdemoros 7A: 32, M1 VA7A-95; 33, M2 VA7A-233; 34, m1 VA7A-262; 35, m2 VA7A-271. From Valdemoros 1A: 36, M1 VA1A-42; 37, M2 VA1A-55; 38, M3 VA1A-68; 39, m1 VA1A-335; 40, m2 VA1A-360; 41, m3 VA1A-34. From Valdemoros 7B: 42, M1 VA7B-481; 43, M2 VA7B-529; 44, m1 VA7B-538; 45, m2 VA7B-560. From Valdemoros 7C: 46, M1 VA7C-877; 47, M2 VA7C-1314; 48, m1 VA7C-1332; 49, m2 VA7C-1369. From Las Umbrias 1: 50, M1 LUM1-110; 51, M2 LUM1-121; 52, m1 LUM1-137; 53, m2 LUM1-148. All of the teeth are at the same magnification. Scale bar equals 1 mm. Right side specimens underlined.

Species	Element	Sites	Length						Width				
			T. N.	N.	min	mean	max	σ	N.	min	mean	max	σ
M. gersii	M1	LUM20	34	24	1,42	1,54	1,62	0,06	30	0,90	1,00	1,09	0,05
M. gersii		LP4C	8	5	1,51	1,61	1,72	0,1	8	0,89	1,02	1,12	0,08
M. gersii		LUM19	33	8	1,48	1,56	1,66	0,05	13	0,95	1,01	1,07	0,04
M. gersii		LP4BA	37	21	1,56	1,61	1,67	0,03	27	0,99	1,05	1,11	0,03
M. gersii		LP4B	57	44	1,51	1,62	1,74	0,05	56	0,93	1,02	1,12	0,04
M. gersii		LP4A	25	23	1,49	1,65	1,82	0,07	22	0,93	1,02	1,09	0,05
M. gersii		LUM14	21	13	1,49	1,57	1,64	0,05	16	0,94	1,00	1,08	0,04
M. gersii		LUM18	9	3	1,48	1,50	1,51		6	0,90	0,94	1,00	0,03
M. gersii		LUM17	17	12	1,45	1,55	1,64	0,06	13	0,92	0,96	1,03	0,03
M. gersii		LUM12	44	16	1,34	1,53	1,67	0,08	19	0,90	0,97	1,05	0,04
M. gersii		LUM16	37	22	1,41	1,55	1,66	0,07	28	0,93	0,98	1,07	0,04
M. gersii		LUM11	70	38	1,47	1,58	1,70	0,05	48	0,90	0,99	1,06	0,04
M. gersii		LUM10	18	10	1,54	1,57	1,59	0,02	10	0,97	1,01	1,08	0,04
M. gersii		LUM9	16	5	1,48	1,54	1,62	0,06	5	0,98	1,01	1,03	0,02
M. gersii		LUM8	27	12	1,48	1,56	1,64	0,05	14	0,93	1,00	1,06	0,04
M. gersii		LUM7	23	7	1,51	1,57	1,62	0,04	11	0,93	1,00	1,06	0,04
M. gersii		VA7G	5	2	1,53		1,55		3	0,99	1,01	1,03	
M. gersii		VA7F	18	11	1,42	1,55	1,75	0,09	14	0,90	0,98	1,05	0,04
M. gersii		VA7E	26	18	1,40	1,53	1,64	0,08	20	0,87	0,99	1,07	0,06
M. gersii		LUM5	9	5	1,51	1,56	1,61	0,04	5	0,98	1,03	1,00	0,05
M. gersii		LUM4	20	7	1,43	1,51	1,57	0,05	13	0,95	0,99	1,06	0,03
M. gersii		VA7D	7	3	1,48	1,52	1,56		4	0,96	0,98	1,00	
M. gersii		LUM3	18	7	1,43	1,50	1,57	0,04	11	0,87	0,97	1,05	0,06
M. gersii		VR11	6	1		1,56			3	0,96	0,99	1,00	
M. gersii		LUM2	10	6	1,48	1,55	1,68	0,09	6	0,91	0,98	1,02	0,04
M.collongensis		LUM1	12	5	1,42	1,48	1,57	0,06	7	0,88	0,97	1,03	0,05
M.collongensis		VA3F	29	13	1,42	1,49	1,57	0,05	18	0,84	0,94	1,01	0,05
M.collongensis		VA3E	55	12	1,45	1,53	1,65	0,07	26	0,89	0,97	1,05	0,04
M.collongensis		VA7C	38	25	1,35	1,47	1,59	0,06	29	0,88	0,96	1,04	0,04
M.collongensis		VA7B	36	15	1,38	1,48	1,58	0,06	18	0,87	0,96	1,05	0,05
M.collongensis		VA1A	28	17	1,36	1,47	1,61	0,06	19	0,88	0,95	1,03	0,04
M.collongensis		VA7A	23	15	1,34	1,46	1,54	0,05	18	0,86	0,95	1,02	0,05
M.collongensis		VA8B	6	1		1,51			2	0,96		1,00	
M.collongensis		VA8C	6	3	1,48	1,53	1,57		4	0,93	0,96	0,97	
M.collongensis		VR8C	59	25	1,34	1,48	1,56	0,05	34	0,85	0,95	1,01	0,03
M.collongensis		VR8B	60	31	1,34	1,46	1,65	0,07	47	0,84	0,94	1,08	0,05
M.collongensis		CS2B	1	1		1,36			1		0,86		
M.collongensis		CS1A	69	19	1,30	1,49	1,61	0,07	27	0,82	0,93	1,01	0,04
M.collongensis		VR7	89	41	1,32	1,47	1,59	0,05	62	0,87	0,93	1,00	0,03
M.collongensis		VA3D	50	10	1,41	1,45	1,53	0,04	19	0,84	0,95	1,02	0,05

Table 6.1. Descriptive statistics of the upper first molar of the species *Megacricetodon collongensis* and *M. gersii* from the Calatayud-Montalbán Basin. Abbreviations: T.N., total number of teeth; N., number of teeth measured; min, minimum; max, maximum; δ, standard deviation.

				Length					Width				
Species	**Element**	**Sites**	**T. N.**	**N.**	**min**	**mean**	**max**	**σ**	**N.**	**min**	**mean**	**max**	**σ**
M. gersii		LUM20	29	19	1,08	1,16	1,22	0,04	23	0,92	1,00	1,07	0,04
M. gersii		LP4C	8	8	1,07	1,11	1,23	0,05	6	0,90	0,96	1,03	0,05
M. gersii		LUM19	16	10	1,09	1,14	1,20	0,05	10	0,91	0,99	1,06	0,04
M. gersii		LP4BA	50	22	1,03	1,14	1,19	0,04	24	0,90	0,97	1,03	0,04
M. gersii		LP4B	47	44	1,00	1,11	1,21	0,05	43	0,91	0,98	1,05	0,04
M. gersii		LP4A	14	13	0,98	1,09	1,23	0,06	12	0,92	0,98	1,05	0,04
M. gersii		LUM14	21	16	1,02	1,10	1,16	0,03	14	0,89	0,94	0,99	0,03
M. gersii		LUM18	8	6	1,04	1,12	1,19	0,06	5	0,91	0,98	1,05	0,05
M. gersii		LUM17	16	10	1,02	1,11	1,19	0,06	11	0,88	0,96	1,01	0,04
M. gersii		LUM12	34	18	1,03	1,11	1,21	0,04	17	0,90	0,95	1,02	0,03
M. gersii		LUM16	36	24	1,06	1,13	1,18	0,04	28	0,91	0,97	1,08	0,04
M. gersii		LUM11	68	44	1,05	1,12	1,22	0,03	45	0,88	0,97	1,04	0,04
M. gersii		LUM10	11	4	1,09	1,14	1,19		5	0,93	0,97	1,01	0,04
M. gersii		LUM9	10	7	1,06	1,13	1,22	0,06	6	0,93	0,99	1,04	0,05
M. gersii		LUM8	24	12	1,05	1,12	1,17	0,04	13	0,96	0,99	1,05	0,03
M. gersii		LUM7	24	13	1,01	1,09	1,17	0,06	14	0,86	0,97	1,07	0,06
M. gersii		VA7G	4	2	1,13		1,14		3	0,92	0,95	0,98	
M. gersii		VA7F	19	8	1,00	1,08	1,25	0,09	9	0,91	0,95	1,00	0,03
M. gersii		VA7E	19	14	1,07	1,13	1,21	0,04	16	0,88	0,97	1,03	0,03
M. gersii	**M2**	LUM5	6	4	1,11	1,14	1,17		5	0,91	1,00	1,04	0,05
M. gersii		LUM4	24	12	1,03	1,12	1,21	0,06	15	0,86	0,97	1,04	0,04
M. gersii		VA7D	13	10	0,99	1,12	1,19	0,06	11	0,88	0,96	1,02	0,05
M. gersii		LUM3	17	15	1,02	1,08	1,14	0,04	13	0,85	0,93	0,99	0,04
M. gersii		VR11	10	6	1,04	1,13	1,21	0,07	7	0,89	0,94	0,98	0,03
M. gersii		LUM2	7	3	1,05	1,13	1,18		3	0,89	0,96	1,01	
M.collongensis		LUM1	12	10	0,96	1,09	1,21	0,06	10	0,88	0,96	1,05	0,04
M.collongensis		VA3F	32	15	0,97	1,06	1,00	0,05	19	0,84	0,91	1,01	0,05
M.collongensis		VA3E	43	21	0,95	1,04	1,13	0,04	23	0,82	0,89	0,97	0,04
M.collongensis		VA7C	32	20	1,02	1,09	1,16	0,04	24	0,89	0,95	1,01	0,03
M.collongensis		VA7B	26	20	0,99	1,07	1,19	0,05	21	0,85	0,93	0,99	0,04
M.collongensis		VA1A	17	7	1,05	1,10	1,19	0,05	8	0,89	0,95	1,02	0,04
M.collongensis		VA7A	12	6	1,04	1,09	1,13	0,04	7	0,85	0,94	1,00	0,05
M.collongensis		VA8B	9	6	1,03	1,08	1,12	0,04	6	0,87	0,93	0,99	0,04
M.collongensis		VA8C	11	6	1,04	1,08	1,12	0,03	5	0,89	0,94	0,99	0,04
M.collongensis		VR8C	48	28	0,96	1,07	1,17	0,05	28	0,84	0,93	1,01	0,04
M.collongensis		VR8B	63	42	0,97	1,05	1,14	0,04	42	0,85	0,91	1,01	0,04
M.collongensis		CS2B	5	4	0,95	1,00	1,03		4	0,87	0,91	0,95	
M.collongensis		CS1A	82	33	0,95	1,03	1,12	0,04	35	0,79	0,91	1,03	0,05
M.collongensis		VR7	87	56	0,98	1,06	1,17	0,04	56	0,82	0,90	1,00	0,04
M.collongensis		VA3D	49	34	0,94	1,05	1,18	0,05	34	0,83	0,90	0,96	0,03

Table 6.2. Descriptive statistics of the upper second molar of the species *Megacricetodon collongensis* and *M. gersii* from the Calatayud-Montalbán Basin. Abbreviations: T.N., total number of teeth; N., number of teeth measured; min, minimum; max, maximum; δ, standard deviation.

Species	Element	Sites	Length						Width				
			T. N.	N.	min	mean	max	σ	N.	min	mean	max	σ
M. gersii	m1	LUM20	24	14	1,32	1,45	1,54	0,07	19	0,82	0,92	1,02	0,06
M. gersii		LP4C	9	4	1,44	1,49	1,55	0,06	8	0,80	0,91	1,04	0,07
M. gersii		LUM19	34	17	1,33	1,46	1,54	0,06	22	0,79	0,89	0,95	0,04
M. gersii		LP4BA	46	15	1,41	1,48	1,56	0,05	29	0,84	0,93	0,97	0,04
M. gersii		LP4B	46	36	1,4	1,48	1,6	0,05	46	0,84	0,93	0,98	0,04
M. gersii		LP4A	13	12	1,41	1,5	1,58	0,05	11	0,84	0,94	1,02	0,05
M. gersii		LUM14	31	13	1,35	1,41	1,54	0,05	20	0,82	0,88	0,94	0,03
M. gersii		LUM18	11	4	1,35	1,43	1,49		9	0,84	0,89	0,97	0,04
M. gersii		LUM17	20	13	1,33	1,42	1,49	0,05	16	0,78	0,88	0,97	0,04
M. gersii		LUM12	35	17	1,37	1,42	1,5	0,04	19	0,85	0,88	0,94	0,03
M. gersii		LUM16	31	18	1,33	1,42	1,49	0,05	21	0,82	0,89	0,98	0,04
M. gersii		LUM11	84	49	1,35	1,45	1,53	0,04	64	0,83	0,90	0,99	0,03
M. gersii		LUM10	19	9	1,43	1,46	1,51	0,03	10	0,86	0,91	0,97	0,04
M. gersii		LUM9	25	13	1,34	1,42	1,48	0,04	19	0,85	0,91	0,97	0,03
M. gersii		LUM8	27	7	1,4	1,47	1,54	0,05	13	0,85	0,91	0,99	0,05
M. gersii		LUM7	16	5	1,39	1,47	1,51	0,05	8	0,86	0,91	0,97	0,04
M. gersii		VA7G	2	2	1,49	1,51	1,52		2	0,87		0,90	
M. gersii		VA7F	18	6	1,3	1,38	1,47	0,06	9	0,86	0,89	0,92	0,02
M. gersii		VA7E	24	14	1,32	1,41	1,49	0,06	20	0,80	0,89	0,94	0,04
M. gersii		LUM5	6	3	1,36	1,42	1,5		5	0,85	0,92	1,00	0,05
M. gersii		LUM4	24	7	1,3	1,41	1,45	0,05	13	0,85	0,89	0,94	0,03
M. gersii		VA7D	6	3	1,34	1,37	1,4		4	0,84	0,90	0,95	
M. gersii		LUM3	14	5	1,35	1,41	1,51	0,06	8	0,80	0,88	0,96	0,06
M. gersii		VR11	7	1		1,46			3	0,80	0,88	0,94	
M. gersii		LUM2	16	4	1,36	1,41	1,46		7	0,82	0,87	0,92	0,04
M.collongensis		LUM1	10	3	1,31	1,35	1,37		6	0,82	0,86	0,90	0,03
M.collongensis		VA3F	22	12	1,23	1,35	1,46	0,07	14	0,78	0,83	0,88	0,03
M.collongensis		VA3E	59	18	1,33	1,4	1,51	0,05	31	0,83	0,89	0,98	0,04
M.collongensis		VA7C	30	14	1,29	1,37	1,44	0,04	24	0,83	0,88	0,95	0,03
M.collongensis		VA7B	20	11	1,3	1,35	1,42	0,04	12	0,81	0,87	0,95	0,04
M.collongensis		VA1A	27	19	1,26	1,33	1,46	0,05	19	0,77	0,85	0,91	0,03
M.collongensis		VA7A	21	6	1,27	1,35	1,47	0,09	10	0,83	0,86	0,90	0,03
M.collongensis		VA8C	5	2	1,41		1,42		3	0,87	0,88	0,90	
M.collongensis		VA8B	4	2	1,39		1,39		2	0,86		0,88	
M.collongensis		VR8C	45	19	1,24	1,36	1,45	0,05	29	0,77	0,84	0,89	0,03
M.collongensis		VR8B	51	26	1,23	1,33	1,41	0,05	34	0,75	0,84	0,90	0,03
M.collongensis		CS2B	10	3	1,29	1,31	1,32		5	0,79	0,82	0,89	0,04
M.collongensis		CS1A	70	17	1,26	1,33	1,44	0,06	32	0,76	0,85	0,91	0,04
M.collongensis		VR7	86	40	1,23	1,34	1,44	0,05	56	0,74	0,83	0,91	0,04
M.collongensis		VA3D	42	14	1,27	1,34	1,42	0,04	18	0,76	0,83	0,89	0,04

Table 6.3. Descriptive statistics of the lower first molar of the species *Megacricetodon collongensis* and *M. gersii* from the Calatayud-Montalbán Basin. Abbreviations: T.N., total number of teeth; N., number of teeth measured; min, minimum; max, maximum; δ, standard deviation.

				Length					Width				
Species	**Element**	**Sites**	**T. N.**	**N.**	**min**	**mean**	**max**	**σ**	**N.**	**min**	**mean**	**max**	**σ**
M. gersii		LUM20	32	25	1,07	1,15	1,23	0,05	22	0,86	0,95	1,03	0,05
M. gersii		LP4C	12	9	1,00	1,17	1,25	0,08	11	0,84	0,93	1,02	0,06
M. gersii		LUM19	40	23	1,06	1,14	1,22	0,04	24	0,85	0,96	1,04	0,04
M. gersii		LP4BA	38	23	1,06	1,16	1,22	0,04	22	0,90	0,98	1,06	0,04
M. gersii		LP4B	53	42	1,05	1,15	1,22	0,05	53	0,86	0,95	1,08	0,04
M. gersii		LP4A	20	19	0,95	1,13	1,24	0,07	20	0,88	0,95	1,04	0,05
M. gersii		LUM14	30	21	1,04	1,13	1,23	0,04	22	0,86	0,94	1,03	0,04
M. gersii		LUM18	9	6	1,10	1,12	1,14	0,02	5	0,90	0,96	1,06	0,07
M. gersii		LUM17	16	8	1,09	1,12	1,16	0,03	9	0,86	0,94	0,98	0,04
M. gersii		LUM12	40	28	1,03	1,10	1,17	0,05	29	0,80	0,90	1,00	0,05
M. gersii		LUM16	38	24	1,08	1,14	1,22	0,04	25	0,88	0,95	1,05	0,04
M. gersii		LUM11	82	48	1,04	1,13	1,20	0,04	53	0,83	0,92	1,03	0,04
M. gersii		LUM10	9	6	1,07	1,14	1,20	0,06	6	0,89	0,95	1,04	0,05
M. gersii		LUM9	17	10	1,09	1,15	1,21	0,04	14	0,89	0,94	1,03	0,04
M. gersii		LUM8	37	12	1,06	1,14	1,22	0,04	13	0,85	0,95	1,00	0,04
M. gersii		LUM7	13	6	1,10	1,13	1,14	0,02	5	0,88	0,92	0,96	0,04
M. gersii		VA7G	3	3	1,06	1,13	1,18		3	0,90	0,95	1,00	
M. gersii		VA7F	17	7	1,04	1,11	1,19	0,05	10	0,87	0,92	0,97	0,03
M. gersii		VA7E	31	17	1,07	1,13	1,21	0,04	19	0,85	0,93	1,06	0,05
M. gersii	**m2**	LUM5	11	5	1,02	1,10	1,17	0,06	4	0,84	0,95	1,01	
M. gersii		LUM4	19	12	1,02	1,13	1,20	0,05	14	0,86	0,94	1,00	0,04
M. gersii		VA7D	5	4	1,10	1,13	1,15		4	0,90	0,95	0,98	
M. gersii		LUM3	22	8	1,01	1,11	1,23	0,07	11	0,83	0,90	0,97	0,05
M. gersii		VR11	9	6	1,06	1,09	1,12	0,02	6	0,86	0,91	0,94	0,03
M. gersii		LUM2	12	6	1,06	1,15	1,20	0,05	7	0,89	0,94	0,98	0,04
M.collongensis		LUM1	11	6	1,00	1,07	1,14	0,05	7	0,82	0,87	0,93	0,04
M.collongensis		VA3F	22	12	1,02	1,07	1,11	0,03	16	0,82	0,88	0,95	0,04
M.collongensis		VA3E	41	17	0,97	1,07	1,15	0,05	19	0,78	0,87	0,93	0,04
M.collongensis		VA7C	30	19	0,98	1,09	1,15	0,04	19	0,86	0,91	0,95	0,03
M.collongensis		VA7B	36	23	0,99	1,09	1,16	0,04	25	0,82	0,91	0,98	0,04
M.collongensis		VA1A	32	17	1,04	1,10	1,19	0,04	18	0,86	0,92	0,99	0,04
M.collongensis		VA7A	30	15	1,05	1,11	1,17	0,03	16	0,80	0,89	0,96	0,04
M.collongensis		VA8B	3	2	1,02		1,13		2	0,87		0,94	
M.collongensis		VA8C	7	5	1,04	1,07	1,09	0,02	4	0,86	0,94	0,98	
M.collongensis		VR8C	44	23	0,97	1,09	1,16	0,05	26	0,82	0,90	0,97	0,04
M.collongensis		VR8B	45	28	1,00	1,06	1,14	0,03	29	0,84	0,90	0,98	0,04
M.collongensis		CS2B	9	7	0,96	1,03	1,08	0,05	7	0,83	0,87	0,92	0,04
M.collongensis		CS1A	78	16	0,97	1,08	1,13	0,04	24	0,80	0,88	0,93	0,03
M.collongensis		VR7	91	47	0,95	1,05	1,12	0,04	58	0,80	0,87	0,94	0,03
M.collongensis		VA3D	49	22	0,97	1,06	1,16	0,04	23	0,83	0,88	0,99	0,04

Table 6.4. Descriptive statistics of the lower second molar of the species *Megacricetodon collongensis* and *M. gersii* from the Calatayud-Montalbán Basin. Abbreviations: T.N., total number of teeth; N., number of teeth measured; min, minimum; max, maximum; δ, standard deviation.

Species	Element	Sites	Length						Width				
			T. N.	N.	min	mean	max	σ	N.	min	mean	max	σ
M. gersii		LUM20	4	4	0,79	0,83	0,86		4	0,80	0,83	0,85	
M. gersii		LUM19	4	4	0,73	0,79	0,85		4	0,71	0,78	0,84	
M. gersii		LUM18	1	1		0,86			1		0,78		
M. gersii		LUM12	4	1		0,84			2	0,78		0,79	
M. gersii		LUM16	1						1		0,69		
M. gersii		LUM11	6	3	0,77	0,81	0,87		5	0,70	0,74	0,82	0,05
M. gersii		LUM10	4	2	0,70		0,70		3	0,69	0,76	0,80	
M. gersii	**M3**	LUM9	2	2	0,77		0,81		2	0,79		0,80	
M. gersii		LUM8	2	2	0,78		0,79		2	0,82		0,84	
M. gersii		LUM7	2	2	0,78		0,83		2	0,76		0,80	
M. gersii		VA7F	4	3	0,73	0,78	0,83		3	0,77	0,79	0,81	
M.collongensis		VA1A	8	4	0,67	0,73	0,78		5	0,72	0,78	0,82	0,04
M.collongensis		VR8C	3	2	0,72		0,76		3	0,76	0,77	0,79	
M.collongensis		VR7	3	2	0,80		0,87		2	0,79		0,81	
M.collongensis		VA3D	1	1		0,79			1		0,75		

Species	Element	Sites	Length						Width				
			T. N.	N.	min	mean	max	σ	N.	min	mean	max	σ
M. gersii		LUM20	2	2	0,99		1,03		1		0,83		
M. gersii		LUM19	14	7	0,87	0,94	1,00	0,05	10	0,73	0,80	0,89	0,05
M. gersii		LUM12	9	3	0,91	0,92	0,94		4	0,75	0,77	0,79	
M. gersii		LUM16	3	1		0,86			3	0,79	0,82	0,89	
M. gersii		LUM11	8	7	0,92	0,96	1,01	0,03	8	0,75	0,80	0,85	0,04
M. gersii		LUM10	1	1		0,99			1		0,86		
M. gersii		LUM9	3	1		0,93			3	0,78	0,83	0,86	
M. gersii		LUM8	11	7	0,91	0,94	0,96	0,02	8	0,79	0,82	0,86	0,03
M. gersii		LUM7	4	1		0,98			1		0,80		
M. gersii		VA7G	1	1		0,92			1		0,80		
M. gersii		VA7F	3	1		0,89			1		0,78		
M. gersii	**m3**	LUM4	4	2	0,91		0,95		4	0,77	0,80	0,82	
M. gersii		LUM3	5	2	0,85		1,00		4	0,77	0,79	0,81	
M. gersii		LUM2	5	3	0,89	0,93	0,99		4	0,76	0,78	0,80	
M.collongensis		LUM1	1	1		0,90			1		0,73		
M.collongensis		VA3F	3	2	0,85		1,03		2	0,69		0,86	
M.collongensis		VA7C	1	1		0,94			1		0,83		
M.collongensis		VA1A	11	5	0,87	0,90	0,93	0,03	5	0,77	0,79	0,81	0,02
M.collongensis		VA8B	2	1		0,98			1		0,80		
M.collongensis		VR8C	8	6	0,87	0,90	1,01	0,05	7	0,74	0,77	0,80	0,02
M.collongensis		VR8B	6	5	0,86	0,90	0,92	0,03	5	0,71	0,78	0,83	0,04
M.collongensis		VR7	8	5	0,81	0,89	0,96	0,06	6	0,68	0,72	0,77	0,04
M.collongensis		VA3D	7	4	0,82	0,87	0,91		4	0,75	0,76	0,78	

Table 6.5. Descriptive statistics of the upper third molar and lower third molar of the species *Megacricetodon collongensis* and *M. gersii* from the Calatayud-Montalbán Basin. Abbreviations: T.N., total number of teeth; N., number of teeth measured; min, minimum; max, maximum;δ, standard deviation.

Many different *Megacricetodon* samples from the Calatayud-Montalbán Basin have been described as *M. collongensis*. In order to clarify the combination of dental morphologies that we assigned to *M. collongensis*, we described here the material of Vargas 8C. This locality has a good representation of all dental elements and its morphology is a good example of the *M. collongensis* from this basin.

M1: The anterocone is deeply split in most specimens (37/43), of which 31 have a small platform in front of the furrow and four a small cingulum ridge in front of it. In the remaining six, the anterocone is slightly subdivided with a small platform in front of the furrow. The labial cone of the anterocone is larger than the lingual one in 35 specimens, the two cones are equal in size in 12 specimens and in the remaining one the lingual cone is larger than the labial. The anterolophule is connected to the lingual cone of the anterocone in 22 specimens, between the two lobes of the anterocone in 27 and to the labial cone in one. The labial spur of the anterolophule is present in 19 out of 55, incipient in three and absent in 33. The forward paracone is present in five out of 56 specimens, incipient in three and absent in 48. The protolophule is posterior (43/55), posterior almost double (10/55) or double (2/55). The ectoloph is strong in 12 specimens, short in 32, and absent in ten. A lingual mesocingulum that connects the protocone to the hypocone, is present in 14 out of 54 specimens. The mesoloph is medium (41/57) or short (16/57). The ectoloph is connected with the mesoloph in three specimens, there is no connection between the ectoloph and the mesoloph in 42, and there is a mesoloph but the ectoloph is absent in the remaining nine. The metalophule is connected to the posteroloph just behind the hypocone in one, is posterior and the metalophule points backwards in 50, it is posterior and the metalophule points backwards more obliquely delimiting a small posterosinus in two, it is posterior almost double in one and it is disconnected in one. (Appendix 6.1. Table 1-12).

M2: The protolophule is anterior in 23 specimens, is anterior almost double in 19, is transverse in one, is posterior almost double in one, and it is double in three. The ectoloph is strong in 30, it is short in 11 and double in the remaining six. In three out of 45 there is a lingual mesocingulum that connects the protocone with the hypocone. The mesoloph is long in six, medium in 35, and short in seven specimens. The ectoloph is connected with the mesoloph in 21 out of 47, and there is no connection between the ectoloph and the mesoloph in 26. The metalophule is anterior (34/45), anterior almost double (3/45), transverse (3/45), points backwards reducing the posterosinus (3/45) or double (2/45). (See Appendix 6.1. Table 13-20).

M3: The lingual anterolophule is well developed in one specimen and is incipient in the remaining two. The protolophule is always anterior and the paracone is always well developed. The metalophule is connected to the neo-entoloph in the three specimens. (Appendix 6.1. Table 21).

m1: The anteroconid is rounded in all the specimens. It is simple in 32 out of 36, and it is slightly subdivided in the remaining four. The antero-lingual cingulid is present in six specimens, incipient in two and absent in 30. Only one specimen (1/36) has an incipient antero-labial cingulid. Three out of 38 have an incipient labial spur of the anterolophulid. The metalophulid is anteriorly connected in 38 specimens and it is disconnected in two. The mesolophid is long (1/42), medium (4/42), short (34/42) or absent (3/42). (Appendix 6.1. Table 22-28).

m2: The lingual anterolophulid is long (19/38), short (17/38) or absent (2/38). The mesoloph is short in 27 out 40 specimens and absent in the remaining 13. (Appendix 6.1. Table 29-30).

m3: The lingual anterolophulid is long in four specimens, short in two, and absent in the remaining one. The mesolophid is present in two and absent in six. (Appendix 6.1. Table 31-32).

Discussion on Megacricetodon collongensis

The assemblages of *Megacricetodon collongensis* from the Calatayud-Montalbán Basin show similar distribution of dental characters (Appendix 6.1). The dental morphology of these assemblages is characterized by upper first molars having the anterocone deeply subdivided in most of the specimens, occasionally having an entomesoloph (crest inside the sinus that starts from the entostyl), and a lingual mesocingulum that connects the hypocone to the anterocone in more than 20% of the specimens, medium or short mesoloph in the M1 and M2; occasionally M2 with double ectoloph; lower first molar with a simple anteroconid in 80% of the specimens, short mesolophid; lingual anterolophid almost always present in the m2 and m3; m2 with short or absent mesolophid; and m3 occasionally with mesolophid.

The differences in dental size among the *Megacricetodon* assemblages are also small, being some slightly larger differences between localities probably due to sampling (see Figure 6.2 and ANOVAS in Appendix 6.2 Table 1-5).

The Spanish *Megacricetodon collongensis* differs from *M. alvarezae* from local zone Dc in size and dental morphology. *Megacricetodon collongensis* is smaller than *M. alvarezae* and morphologically differs from the latter by its upper first molar having entomesoloph and longer ectoloph; M2 with double ectoloph and higher percentage of double protolophule; m1 with less subdivided anteroconid (simple anteroconid in 80% of the specimens) and

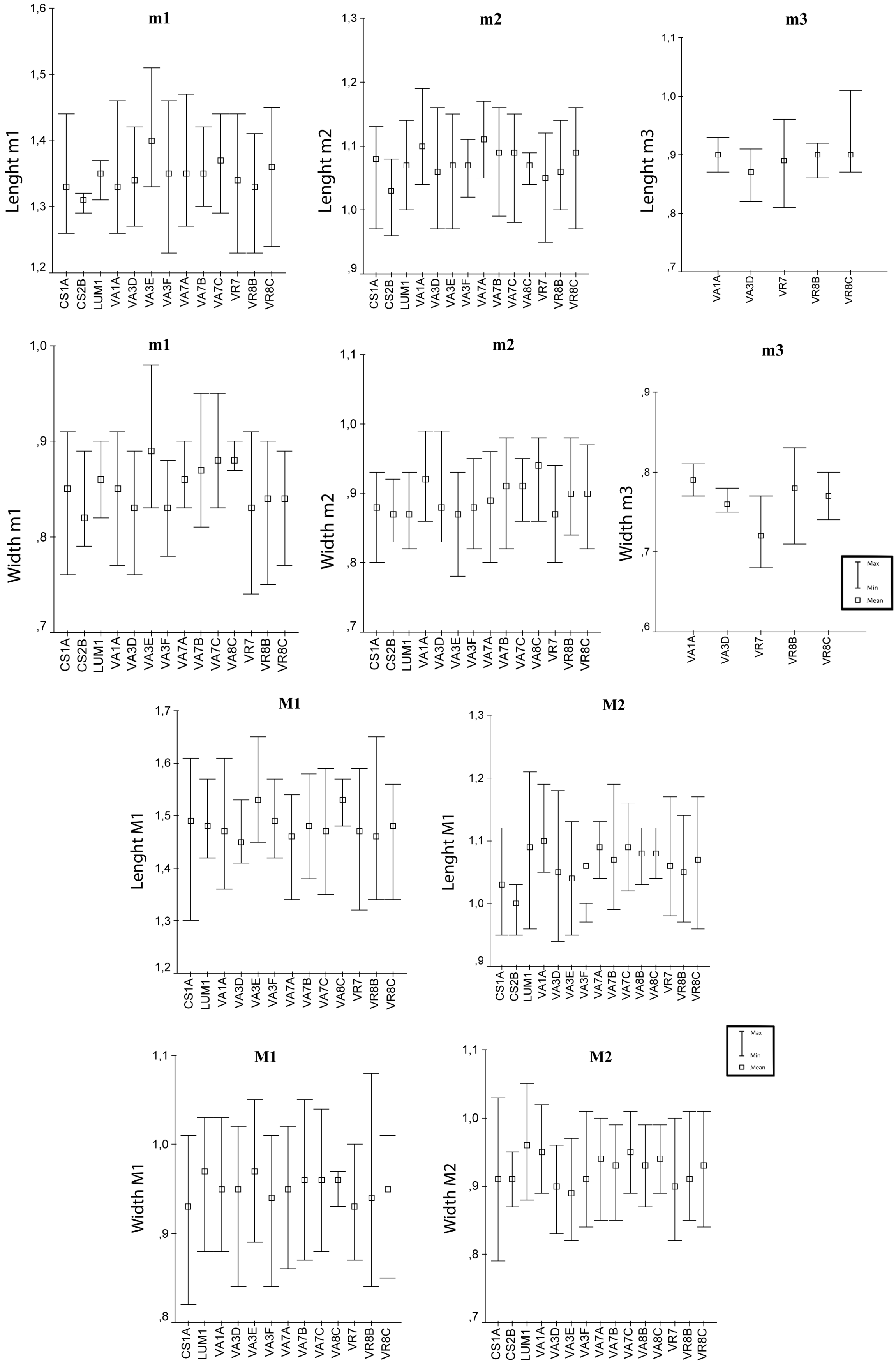


Figure 6.2. Distribution of the Length and Width ranges charts of the upper and lower dental elements for the successive assemblages of *Megacricetodon collongensis* from the Calatayud-Montalbán Basin. Abbreviations: VA3D, Valdemoros 3D; VR7, Vargas 7; CS1A, Casetón 1A; CS2B, Casetón 2B; VR8B, Vargas 8B; VR8C, Vargas 8C; VA8C, Valdemoros 8C; VA8B, Valdemoros 8B; VA7A, Valdemoros 7A; VA1A, Valdemoros 1A; VA7B, Valdemoros 7B; VA7C, Valdemoros 7C; VA3F, Valdemoros 3F; LUM1, Las Umbrias 1.

lower percentage of presence of the labial spur of the anterolophule; and m2 and m3 with longer lingual anterolophid and mesoloph.

These *Megacricetodon* assemblages from the lower zone Dd, and despite the close similarities in size and general morphology, can be clearly distinguished from the material of *M. primitivus* from older localities. *Megacricetodon collongensis* differs from *M. primitivus* by having the M1 with higher percentage of ectoloph and entomesoloph, the lower percentage of lingual mesocingulum that connects the hypocone and the anterocone, the higher percentage of connection between the ectoloph and the mesoloph; M2 with double ectoloph, higher percentage of double metalophule; and lower first molars with higher percentage of double anteroconid.

Megacricetodon collongensis from Vieux-Collonges and the *Megacricetodon assemblages* from the lower part of the local Dd in the Calatayud-Montalbán Basin show similar size (see Table 6.1-6.5) and morphological dental characteristics (M1 occasionally with entomesoloph, and with a lingual mesocingulum that connects the hypocone to the anterocone in more than 20% of the specimens; m1 with simple anteroconid in more than 75% of the specimens; and m3 occasionally with mesolophid). Therefore, based on the morphological similarities with the Vieux Collonges type material (Mein, 1958), we have assigned these assemblages from the Calatayud-Montalbán Basin to *Megacricetodon collongensis.* Nevertherless, *M. collongensis* should be treated with care, due to the high variability in its type locality, since practically any small-sized *Megacricetodon* comes at the margins of variation of this sample (Maridet, 2003). As discussed previously, this high morphometric variability of the Vieux-Collonges assemblages, might be probably do to its karstic origin that could represent a mixing of levels and species.

***Megacricetodon collongensis* in Other Spanish Basins**

In the Ebro Basin, the locality of Tarazona was assigned to *M. collongensis* (Valdés et al., 1986) and correlated to local zone Dd (Álvarez-Sierra et al., 2006). We agree with this allotment, based on the similar size and morphology shared by the material from Tarazona and the Calatayud-Montalbán Basin.

The *Megacricetodon* from Mira (Mira Basin) was assigned to *M. collongensis* by Agustí et al., (1988). Unfortunately the material is very scarce (only seven teeth), and the size is intermediate between *M. collongensis* and *M. gersii*. However, the faunal association (*Democricetodon* cf. *koenigswaldi*, *Armantomys aragonensis*, *Microdyromys koenigswaldi*, *Simplomys simplicidens*) suggest the lowermost part of the local zone Dd. Therefore, the *Megacricetodon* is assigned to *M. collongensis*.

After the revision of the European localities, we consider that the geographical distribution of the species *Megacricetodon collongensis* is Southwester Europe (Spain and France).

Megacricetodon gersii Aguilar, 1980

(Figs. 6.3:1–42, Figs. 6.4: 1–37)

Cricetodon minor collongensis from Las Planas 4A and Las Planas 4B in Freudenthal, 1963: 30-32.

Megacricetodon minor collongensis from Las Planas 4A and Las Planas 4B in Daams et al., 1977: 48, 52, fig. 3, 4, 5.

Megacricetodon collongensis from Las Planas 4A, Las Planas 4B and Las Planas 4C in Daams, 1981.

Megacricetodon collongensis from Las Planas 4A, Las Planas 4B and Las Planas 4C in Freudenthal & Cuenca Bescos, 1984.

Megacricetodon crusafonti Pérez et al., 1985: 408-409.

Megacricetodon collongensis from Las Planas 4A, Las Planas 4B and Las Planas 4C in Daams et al., 1987: 304, fig. 5.

Megacricetodon collongensis from Las Planas 4A, Las Planas 4B and Las Planas 4C in Daams and Freudenthal, 1988a.

Megacricetodon collongensis from Las Planas 4A, Las Planas 4B and Las Planas 4C in Daams & Freudenthal, 1988b: 14, fig. 8.

Megacricetodon collongensis from uppermost part Dd and E in Daams et al., 1998: 627, fig. 1.

Megacricetodon collongensis from uppermost part Dd and E in Daams et al., 1999: 126, fig. 10, 127.

Megacricetodon collongensis from uppermost part Dd and E in Alcalá et al., 2000: 327, fig. 3.

Megacricetodon collongensis Luis & Hernando, 2000.

Megacricetodon collongensis from uppermost part Dd and E in López Olmedo et al., 2004: 95, fig. 8.

Megacricetodon collongensis Álvarez-Sierra et al., 2006: 7-8, table 1, plate 1 fig. 8, 9.

Megacricetodon collongensis Hernández Fernández et al., 2006:274, 282.

Megacricetodon collongensis from E in Sesé, 2006: 441,447, fig.4.

Megacricetodon collongensis Murelaga et al., 2008:398-399, tabla 2, fig. 4.

Megacricetodon collongensis Hernández-Ballarín et al., 2010: 152-154, fig. 3.

Megacricetodon collongensis Menéndez Gamella et al., 2010: 191-192, 194-195, fig.6.

Megacricetodon "collongensis" and *Megacricetodon "collongensis-gersii"* Hernández-Ballarín et al., 2011: 176-180, tabla 1, fig. 3.

Megacricetodon collongensis from uppermost part Dd and E in van der Meulen et al., 2012: 166, figs. 3, 5, 6.

Holotype: Mandible m1-m2 left B-Sa 11.208 (Baudelot, 1972: pl 14, fig. 1).

Type Locality: Sansan (France).

Stratigraphical distribution: Upper part of local zone Dd and local zone E, middle Aragonian, middle Miocene.

Geographical distribution: Portugal, Spain, France, Switzerland.

Measurements: Tables 6.1-6.5.

The description of *Megacricetodon gersii* from the Calatayud-Montalbán Basin is based on the material of Las Umbrias 11. The *Megacricetodon* of this locality is very representative of the *Megacricetodon gersii* from this basin.

M1: The anterocone is deeply subdivided (6/52) or have a shallow subdivision (46/52). In three out of 52 there is not a platform or a cingulum in front of the anterocone, in 35 there is a small platform in front of the anterocone, and in the remaining 14 there is a platform and a small cingulum ridge in front of the anterocone. The labial cone of the anterocone is larger than the lingual one in 48specimens, while the two cones are equal in size in six specimens. The anterolophule is connected to the lingual cone of the anterocone in 19 specimens, between the two lobes of the anterocone in 36 and to the labial cone in one. The labial spur of the anterolophule is present in seven specimens, incipient in six and absent in 54. The protolophule is posterior (61/67), posterior almost double (2/67) or double (4/67). In 27/66 the ectoloph is strong, in31 is short and in eight is absent. A lingual mesocingulum that connects the protocone to the hypocone, is present in eight specimens (8/63). The mesoloph is long in one, medium in 17, short in 47 and absent in one. In 27 out of 65, the ectoloph is connected with the mesoloph, in 31 there is no connection between the ectoloph and the mesoloph, in six there is a mesoloph but the ectoloph is absent and in the remaining one there is neither a mesoloph nor an ectoloph. The metalophule points forward and it is connected to the entoloph in front of the hypocone (1/59), is transverse in five (5/59), is connected to the posteroloph just behind the hypocone in seven (7/59), is posterior and the metalophule points backwards in 43 (43/59), is posterior almost double in one (1/59) or it is double (2/59). (Appendix 6.1. Table 1-12).

M2: The protolophule is anterior in 23 specimens, is anterior almost double in five, is transverse in one, is transverse but it is connected to the entoloph behind the protocone in one, the entoloph is connected to the protocone indirectly through paracone and protolophule in 12, it is double in 21 and the protolophule points backwards and connects

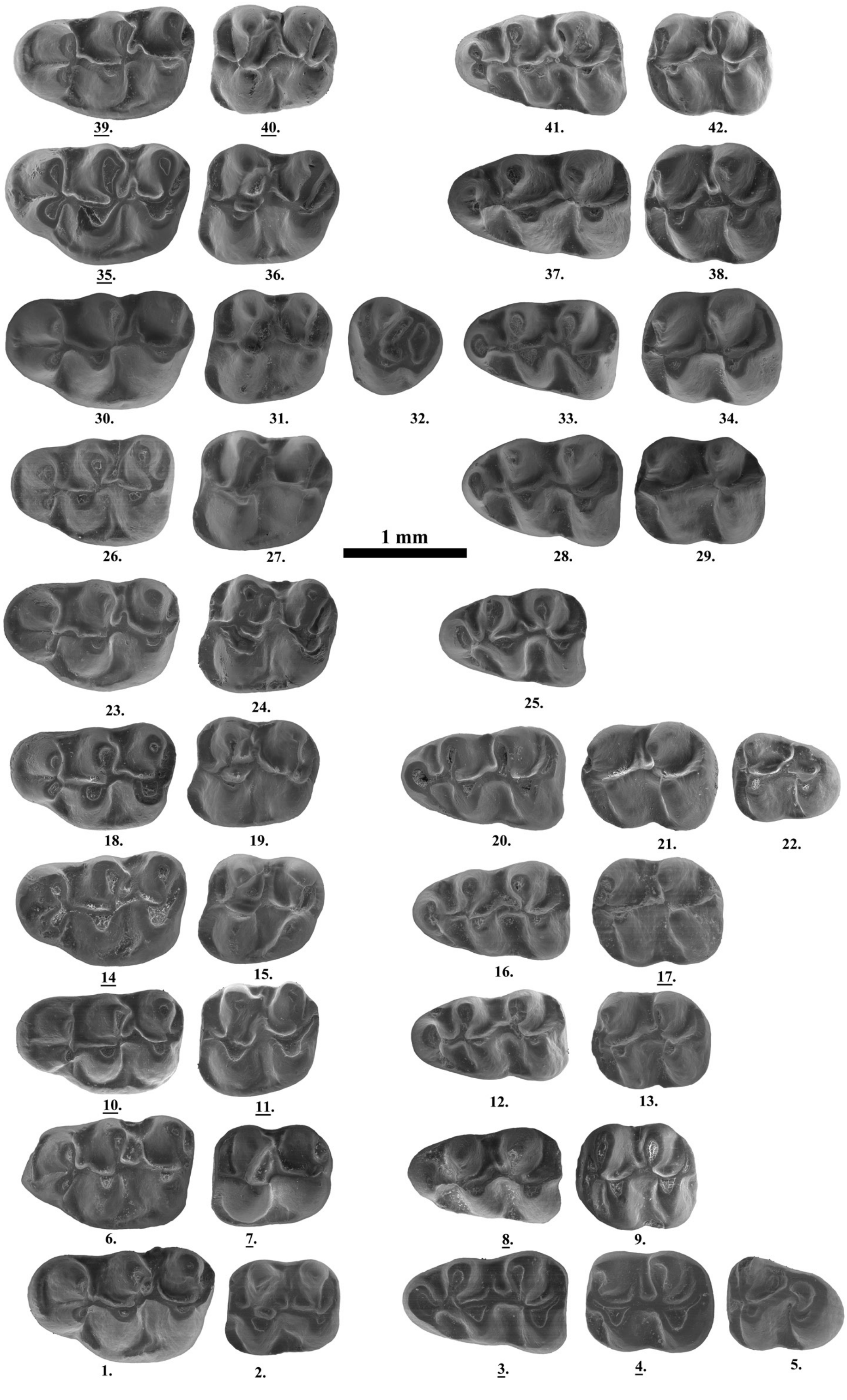


Figure 6.3. *Megacricetodon gersii* from the Calatayud-Montalbán Basin. From Las Umbrias 2: 1, LUM2-132 M1 left; 2, LUM2-138 M2 left; 3, LUM2-152 m1 right; 4, LUM2-169 m2 right. 5, LUM2-172 m3 left. From Vargas 11: 6, VR11-171 M1 left; 7, VR11-182 M2 right; 8, VR11-188 m1 right; 9, VR11-193 m2 left. From Las Umbrias 3: 10, LUM3-795 M1 right; 11, LUM3-1071 M2 right; 12, LUM3-1080 m1 left; 13, LUM3-1091 m2 left. From Valdemoros 7D: 14, VA7D-130 M1 right; 15, VA7D-137 M2 left; 16, VA7D-147 m1 left; 17, VA7D-155 m2 right. From Las Umbrias 4: 18, LUM4-435 M1 left; 19, LUM4-465 M2 left; 20, LUM4-481 m1 left; 21, LUM4-501 m2 left; 22, LUM4-524 m3 left. From Las Umbrias 5: 23, LUM5-158 M1 left; 24, LUM5-166 M2 left; 25, LUM5-170 m1 left. From Valdemoros 7E: 26, VA7E-543 M1 left; 27, VA7E-591 M2 left; 28, VA7E-566 m1 left; 29, VA7E-611 m2 left. From Valdemoros 7F: 30, VA7F-160 M1 left; 31, VA7F-222 M2 left; 32, VA7F-236 M3 left; 33, VA7F-241 m1 left; 34, VA7F-259 m2 left. From Valdemoros 7G: 35, VA7G-91 M1 right; 36, VA7G-94 M2 left; 37, VA7G-93 m1 left; 38, VA7G-100 m2 left. From Las Umbrias 7: 39, LUM7-78 M1 right; 40, LUM7-108 M2 right; 41, LUM7-24 m1 left; 42, LUM7-117 m2 left. Right side specimens underlined. All of the teeth are at the same magnification. Scale bar equals 1 mm.

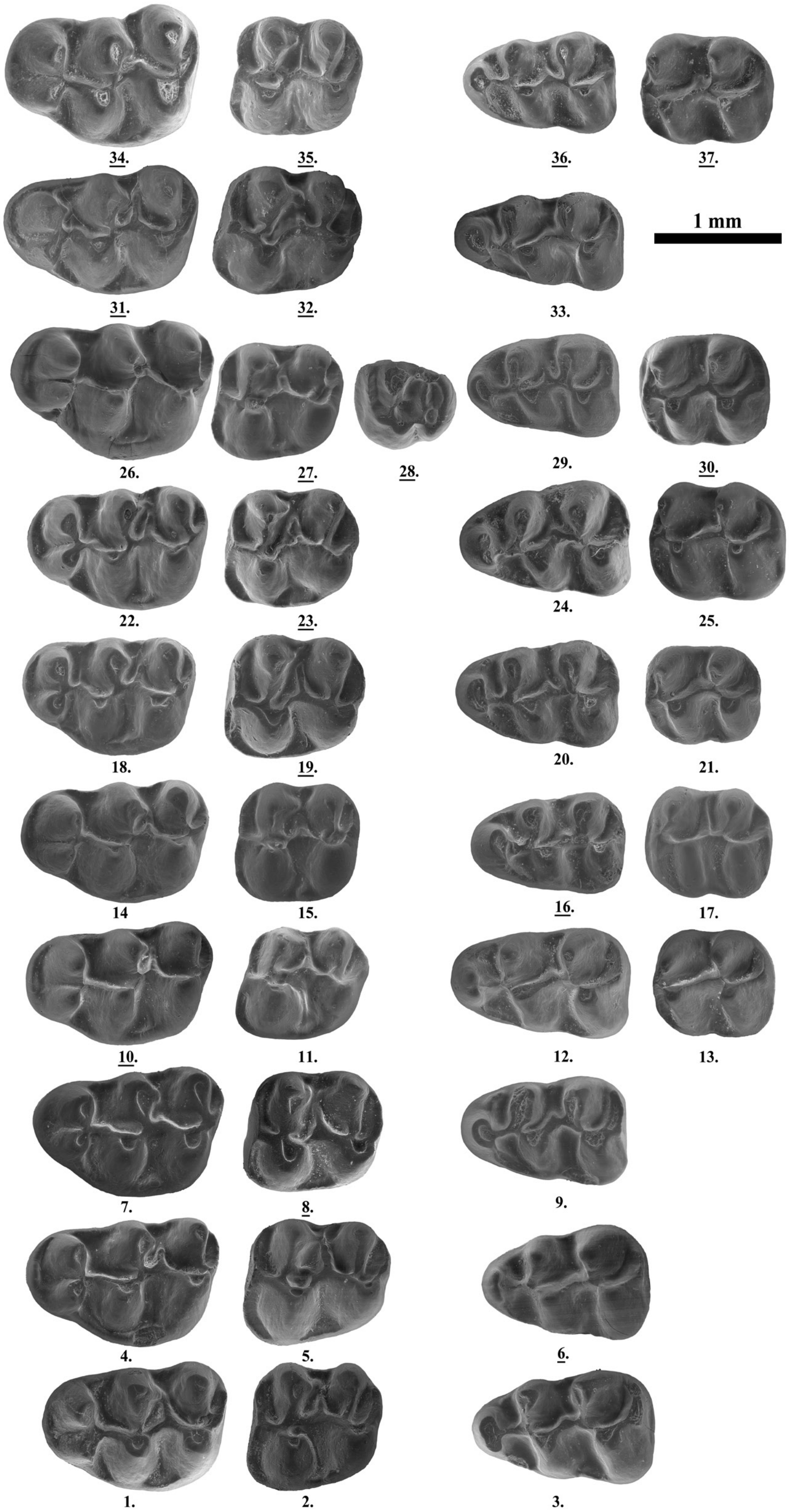


Figure 6.4. *Megacricetodon gersii* from the Calatayud-Montalbán Basin. From Las Umbrias 8: 1, LUM8-201 M1 left; 2, LUM8-304 M2 left; 3, LUM8-84 m1 left. From Las Umbrias 9: 4, LUM9-88 M1 left; 5, LUM9-153 M2 left; 6, LUM9-125 m1 right. From Las Umbrias 10:7, LUM10-34 M1 left; 8, LUM10-50 M2 left. 9, LUM10-62 m1 left. From Las Umbrias 11: 10, LUM11-121 M1 right; 11, LUM11-338 M2 left; 12, LUM11-170 m1 left. 13, LUM11-401 m2 left. From Las Umbrias 16: 14, LUM16-108 M1 left; 15, LUM16-140 M2 left; 16, LUM16-190 m1 left; 17, LUM16-201 m2 left. From Las Umbrias 12: 18, LUM12-74 M1 left; 19, LUM12-222 M2 right; 20, LUM12-118 m1 left. 21, LUM12-230 m2 left. From Las Umbrias 17: 22, LUM17-39 M1 left; 23, LUM17-64 M2 right; 24, LUM17-65 m1 left. 25, LUM17-86 m2 left. From Las Umbrias 18: 26, LUM18-54 M1 left; 27, LUM18-64 M2 right; 28, LUM18-108 M3 right; 29, LUM18-68 m1 left; 30, LUM18-83 m2 right. From Las Umbrias 19: 31, LUM19-290 M1 right; 32, LUM19-20 M2 right; 33, LUM19-22 m1 left. From Las Umbrias 20: 34, LUM20-57 M1 right; 35, LUM20-98 M2 right; 36, LUM20-73 m1 right; 37, LUM20-117 m2 right. Right side specimens underlined. All of the teeth are at the same magnification. Scale bar equals 1 mm.

behind the protocone in the remaining one. The ectoloph is strong in 49 out of 68, and it is short in the remaining 19. The mesoloph is long in two, medium in 23 and short in 42. The ectoloph is connected with the mesoloph in 30, and there is no connection between the ectoloph and the mesoloph in 37. The metalophule is disconnected (2/60), anterior (41/60), transverse (4/60), points backwards and it is connected to the posteroloph, just behind the hypocone (5/60), it is posterior almost double (1/60) or double (7/60). (Appendix 6.1. Table 13-20).

M3: The paracone is always well developed. The metalophule is absent (3/6), is connected to the anterior arm of the hypocone (1/6) or it is connected to the anterior arm of the hypocone and the protolophule (2/6). (Appendix 6.1. Table 21).

m1: The anteroconid is rounded (53/65) or elongated (12/65). In 37 out of 65 specimens the anteroconid is simple, in 19 is slightly subdivided, in eight is 8-shaped with a deep furrow, and in the remaining one the anteroconid is deeply split. In five specimens (5/67) there is an antero-lingual cingulid, and in three is incipient. The antero-labial cingulid is present in one (1/66), incipient in other one (1/66) and absent in 64 (64/66). A labial spur of the anterolophulid is present in one specimen, incipient in one and absent in 72. The metalophulid is anteriorly connected in 72 specimens, is anteriorly connected with a second connection almost complete in one, and is double in three. The mesolophid is medium (6/78), short (66/75) or absent (6/78). The Ectomesolophid is always absent. (Appendix 6.1. Table 22-28).

m2: The lingual anterolophulid is long (8/70), short (58/70) or absent (4/70). The mesolophid is medium in three specimens, short in 64 and absent in 11. (Appendix 6.1. Table 29-30).

m3: The lingual anterolophulid is short in the eight specimens. The mesolophid is present in two specimens and absent in the remaining six. (Appendix 6.1. Table 31-32).

Discussion on Megacricetodon gersii

As we previously noted, the differences between the *Megacricetodon* assemblages of the lower and upper part of the local zone Dd, allow us to discriminate two successive forms of the same lineage (see Appendix 6.1 and Tables 6.1-6.5).

The *Megacricetodon* material from the upper part of the biozone Dd and E in Calatayud-Montalbán Basin is characterized by upper first molars having an anterocone deeply subdivided, occasionally having a entomesoloph, short or medium mesoloph in the M1 and M2; lower first molar with an anteroconid simple, slightly subdivided or 8-shaped, absent ectomesolophid, short or absent mesolophid in the m1 or m2; and occasionally in the m3. This dental morphology remains rather constant through time (see Appendix 6.1).

The dental size of all the assemblages assigned to this species remains unchanged, except for the material from the younger localities, where the *Megacricetodon* is slightly larger (see Tables 6.1-6.5, figure 6.5 and Appendix 6.3).

Megacricetodon assemblages from the upper zone Dd and zone E in the Calatayud-Montalbán Basin are larger than *M. primitivus* and smaller than *M. vandermeuleni*. Moreover, *Megacricetodon alvarezae* from local zone Dc has a similar dimensions but differs by having the upper first molar with lower percentage of anterolophule connected to the middle of the two cones of the anterocone, low presence of long ectoloph, lower percentage of ectoloph connected to the mesoloph in the upper molars; M2 with higher percentage of anterior protolophule, higher percentage of short ectoloph; lower first molar with higher percentage of labial spur of the anterolophid; and absence of mesolophid in the m3.

The Spanish assemblages from the upper zone Dd and zone E are assigned to *Megacricetodon gersii* Aguilar, 1980, owing to their morphological similarities to the French species. Among the main morphological similarities we point out: the deeply subdivided anterocone and the symmetry of the anterocone, the protolophule of the M1, the connection of the ectoloph with the mesoloph in the upper molars, the rounded anteroconid, the metalophulid and the absence of ectomesolophid in the m1, the mesolophid in the lower molars and the lingual anterolophid in the m2 and m3 (see Appendix 6.1 for the distribution of character states).

In the following paragraphs we discuss the *Megacricetodon* assemblages from different Iberian basins that have been assigned or might be assigned to *Megacricetodon gersii.*

Duero Basin: García Moreno (1987) assigned to *M. gersii* the material from Valladolid 1. We do not agree with this allotment considering that both the size and the morphology are closer to the *Megacricetodon* from local zone F.

Ebro Basin: The material from the locality of Villanueva de Huerva was assigned to *Megacricetodon crusafonti* by Pérez et al., (1985). We do not agree with this allotment, both the size and morphology resemble well with *M. gersii*.

The localities of Tarazona 2 and 3 have been correlated to local zone Dd or E (Tarazona 2) or to local zone E (Tarazona 3) (Álvarez-Sierra et al., 2006). The *Megacricetodon* from these localities were allotted to *M. collongensis*. However, the morphology and size of the material, as well as, its stratigraphic correlation at the end of MN 5, is compatible with its assignation to *Megacricetodon gersii* instead to *M. collongensis*.

The locality of Melero 20 has been correlated to local zone E and assigned to *Megacricetodon collongensis* (Murelaga et al., 2008). As in the case of Tarazona, both the

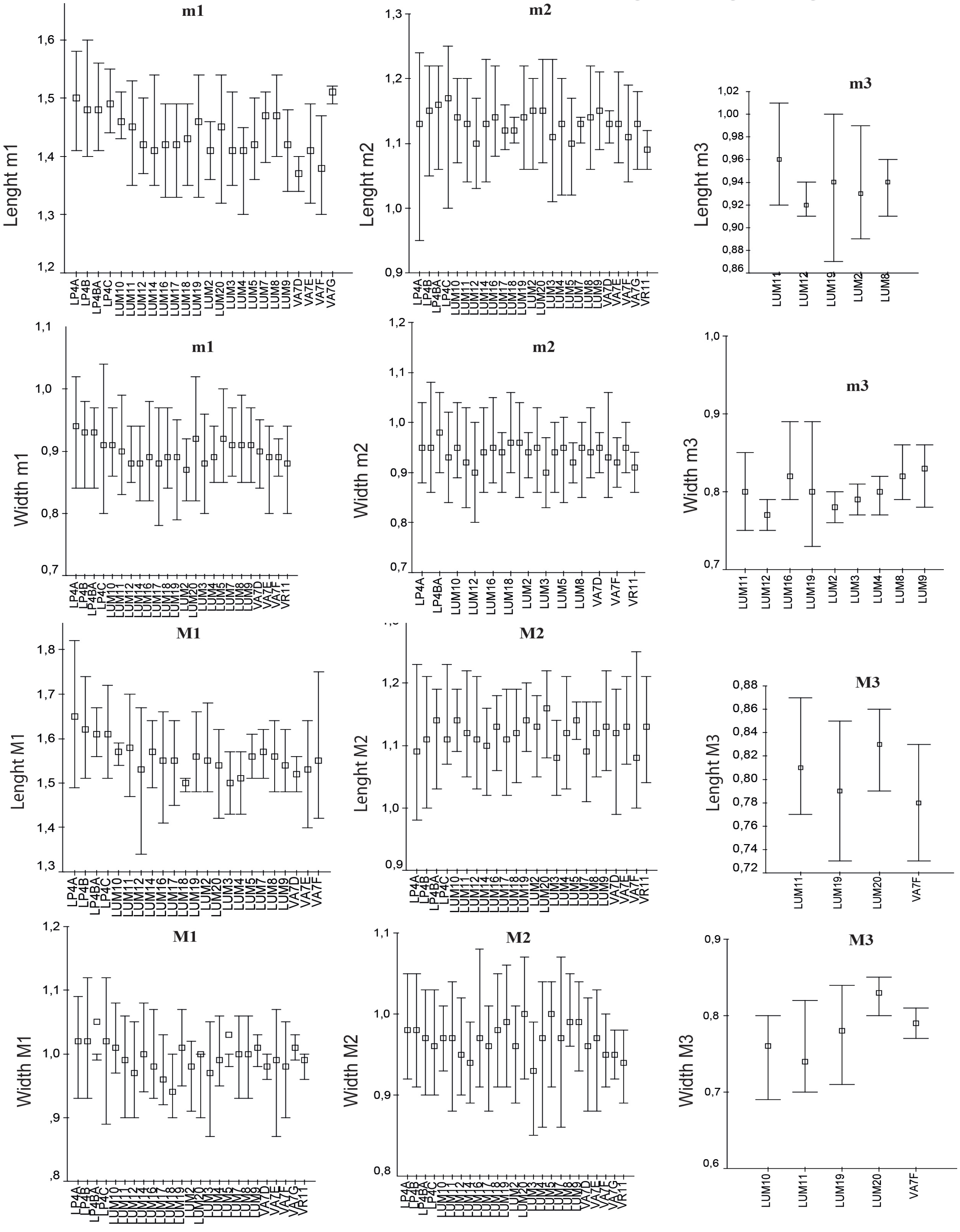


Figure 6.5. Distribution of the Length and Width ranges charts of the upper and lower dental elements for the successive assemblages of *Megacricetodon gersii* from the Calatayud-Montalbán Basin. Abbreviations: LUM2, Las Umbrias 2; VR11, Vargas 11; LUM3, Las Umbrias 3; VA7D, Valdemoros 7D; LUM4, Las Umbrias 4; LUM5, Las Umbrias 5; VA7E, Valdemoros 7E; VA7F, Valdemoros 7F; VA7G, Valdemoros 7G; LUM7, Las Umbrias 7; LUM8, Las Umbrias 8; LUM9, Las Umbrias 9; LUM10, Las Umbrias 10;LUM11, Las Umbrias 11; LUM16, Las Umbrias 16; LUM12, Las Umbrias 12; LUM14, Las Umbrias 14; LP4A, Las Planas 4A, LP4B, Las Planas 4B; LP4BA, Las Planas 4BA; LUM17, Las Umbrias 17; LUM18, Las Umbrias 18; LUM19, Las Umbrias 19; LP4C, Las Planas 4C and LUM20, Las Umbrias 20.

size and morphology of the *Megacricetodon* material, and the correlated age, suggest the allotment to *M. gersii*.

Quesa Basin: The *Megacricetodon* material from the locality of Quesa 2 (Valencia) was assigned to *M. collongensis* and correlated to local zone E by Ruiz-Sánchez et al., (1995). Based on its larger size and morphology, we considered that should be assigned to *M. gersii* instead of *M. collongensis*.

Madrid Basin: The locality of Somosaguas was assigned to *M. collongensis* (Luis & Hernando, 2000) and correlated to local zone E. We suggest its assignation to *M. gersii* based on its size and morphology. The material from Húmera (fossil site very close to Somosaguas) was also allotment to *Megacricetodon collongensis* by Menéndez Gamella et al. (2010). However, we suggest it allotment to *M. gersii*.

Hernández-Ballarín et al. (2010; 2011), studied the *Megacricetodon* material from the localities of El Cañaveral, Arroyo del Olivar, Casa Montero and Somosaguas, correlating the fossil sites in the local zone E. They assigned the material to *Megacricetodon "collongensis"* (El Cañaveral and Arroyo del Olivar) and to *Megacricetodon "collongensis-gersii"* (Casa Montero and Somosaguas). We consider that all this material should be included in the species *M. gersii*, considering that both the size and the morphology are equal to *M. gersii* from the Calatayud-Montalbán Basin. The larger size in the *Megacricetodon* material from the younger localities of the Madrid Basin (Casa Montero, Somosaguas) is consistent with the larger size that appear in the younger localities of the Calatayud-Montalbán Basin (Las Planas 4A, Las Planas 4B, Las Planas 4BA, Las Planas 4C).

Tagus Basin: The *Megacricetodon* material from the locality of Amor (Portugal) was allotment to *M. collongensis* (Antunes & Mein, 1981). Nevertheless, we recommend its assignation to *Megacricetodon gersii*, both for its large sized and for its occurrence with modern cricetids (*Cricetodon*).

With regard to other European basin, *Megacricetodon gersii* has been recognized also in Upper Freshwater Molasse of Switzerland. Kälin & Kempf (2009) assigned to this species, the material from the localities of Rützentobel 550 and 567, Mettlen 4, Zeglingen, Oschgraben, Niderwis, Hutziker Tobel 670m, Schmidrüti, Le Locle Sous, le Stand C-13, Chapt and Grat 930m. In Germany there has been no record of *M. gersii*, presumably because of the absence of fossil record covering the temporal distribution of this species (Heissing, 1997).

Therefore, the known geographical distribution of *Megacricetodon gersii* is Western Europe (Portugal, Spain and France) and Switzerland.

Aguilar (1980; 1995) proposed the lineage *M. collongensis – M. gersii*. He also claimed that this lineage is only recognizable in France, since he thought that the material assigned to *Megacricetodon collongensis* from France and Spain belong to different lineages that evolved independently. Posterior works of this author (Lazzari & Aguilar, 2007) present a different phylogenetic framework for *Megacricetodon*, where there are to different lineages starting at forms that were described formerly as *M. collongensis*. In this way Lazzari & Aguilar (2007), propose two lineages, *M. "collongensis"* (Port-la-Nouvelle) – *M. gersii* – *M. rousillonensis* and the lineage *M. tautavelensis – M. collongensis* (Vieux-Collonges) – *M. rafaeli*.

Based on the morphological similarities between *M. collongensis* from Vieux-Collonges and the *M. collongensis* from the Calatayud-Montalbán Basin, instead to the Port la Nouvelle form, the results presented here support the existence of the lineage *M. collongensis-M. gersii*. This lineage had a geographic distribution in Western Europe (the Iberian Peninsula and France). The extension of the *M. collongensis - M. gersii* lineage to include *M. lemartineli - M. fournasi - M. rousillonensis* proposed by Aguilar (1995) has not been studied in detail and therefore is not proposed here as certain.

6.5. FINAL REMARKS

As mentioned above, *Megacricetodon collongensis* and *M. gersii* are two species of the same lineages. We propose a closely related group of *Megacricetodon*, the "*M. primitivus* group", which includes *M. primitivus, M. alvarezae, .M. collongensis* and *M. gersii*. All the species of this group are characterised by upper first molars having the anterocone deeply subdivided in most of the specimens and a lingual mesocingulum that connects the hypocone to the anterocone in more than 20% of the specimens; lower first molars with a rounded anteroconid and with similar height in the five main cusps of the m1 (see Figure 6.6).

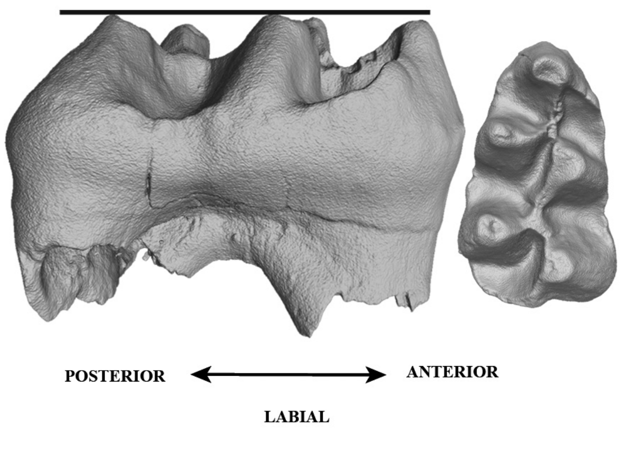


Figure 6.6. Labial and occlusal views of a lower first molar, showing the relative height of the five main cusps. In the "*Megacricetodon primitivus* group" the anteroconid is of similar height than the other cusps (Modified from Oliver & Peláez-Campomanes, 2014).

This group occurred in France during the MN 4, being the first occurrence in the Iberian Peninsula at the local zone Ca (latest MN 4). According to Oliver & Peláez-Campomanes (2014), the migration of the "*M. primitivus* group" would be the third migration wave for the early *Megacricetodon* forms. The small-sized *Megacricetodon primitivus*, appeared during MN 4, in southern France (Gers localities), after *M. bezianensis* (Ginsburg and Bulot, 2000), and reached Spain and Portugal at latest MN 4 (Ginsburg and Bulot, 2000; Oliver and Peláez-Campomanes, in press). During the early MN 5 (latest biozone Db) this species evolves into *M. alvarezae* being, so far, only known from the Iberian Peninsula. In France, *M. primitivus* could be the origin for *M. collongensis* at early MN 5. In Spain the latter species occurs in the lower part of local zone Dd, evolving to *M. gersii* in the upper part of the local zone Dd. The "*M. primitivus* group" would not have reached Central Europe (Switzerland) until latest MN 5 with the species *M. gersii*. Kälin & Kempf (2009) presented a revised chronoglogy of the Northern Alpine Foreland Basin of Switzerland for the middle Miocene. They assigned to *Megacricetodon gersii* the material from the localities Rützentobel 550 and 567, Mettlen 4, Zeglingen, Oschgraben, Niderwis, Hutziker Tobel 670m and Schmidrüti (from Oeschgraben and Mettlen-Weid zones), and the localities of Le Locle Sous le Stand C-13, Chapt and Grat 930m (from Helsighausen zone) equivalents to the Spanish upper Dd and E zones (van der Meulen et al., 2011).

The detailed study of the *Megacricetodon* assemblages from the local zone Dd and E, from the Calatayud-Montalbán Basin, has revealed that *M. gersii* occurred in the Iberian Peninsula in the middle Aragonian (local zone Dd and E) and not in the upper Aragonian (local zone F) as previously thought. This change has important bioestratigraphical and biochronological implications. To date, the first occurrence of *Megacricetodon gersii* has been used as key species to propose biochronological correlations within Europe, especially between the three better studied areas for the lower and middle Miocene, the Upper Freshwater Molasse of the North Alpine Foreland Basin in Switzerland(Bolliger, 1997; Kälin, 1997; Kempf et al., 1997; Kälin & Kempf, 2009), the Upper Freshwater Molasse in Bavaria(Abdul Aziz et al., 2008; 2010), and the Aragonian type area in the Calatayud-Montalbán Basin (Daams et al., 1999; van Dam et al., 2006; van der Meulen et al., 2011; 2012). Kälin & Kempf, (2009) correlated Sansan (the type locality of *M. gersii*) the Swiss locality of Niderwis (14.1 Ma) and with the lower part of the chron C5ACn (14 Ma, local zone E). Van der Meulen et al., (2011), based on the latter correlations, considered that the Swiss *M. gersii* predate its occurrence in Spain, and there is an asynchrony of 400 ky between their occurrences.

According to our results, the first occurrence of *M. gersii* in Western Europe was in the middle part of local zone Dd, whereas in Switzerland would not appear until the Oeschgraben local zone, equivalent to the upper part of the Spanish Dd. Therefore, the use of *M. gersii* event for bioestratigraphical correlations in Europe proposed previously (Daams et al., 1999; van der Meulen et al., 2011) is different to the proposed here. They differ not only in the direction of the migration (West to East instead of being from Switzerland to Spain), but also in the magnitude of the diachrony (approximately 200ky instead of 400 ky).

6.6. CONCLUSIONS

The study and revision of the *Megacricetodon* material from the localities of the local zone Dd and E (middle Aragonian, middle Miocene) from the Calatayud-Montalbán Basin, allowed us to recognize and characterize two successive species within a single lineage, *Megacricetodon collongensis* in the lower part of the local zone Dd and *Megacricetodon gersii* in the upper part of the biozone Dd and E. The change from one species to the next is marked in the Calatayud-Montalbán Basin by an increase in size and several morphological changes on the dental pattern. These changes occurred approximately at the same time of one of the main sedimentological changes in the Basin.

The small-sized *Megacricetodon collongensis* is characterized by having, in most of the upper first molar, an anterocone deeply subdivided, occasionally an entomesoloph, and a lingual mesocingulum that connects the hypocone to the anterocone in more than 20% of the specimens; M2 with double ectoloph; m1 with a simple anteroconid in 80% of the specimens; and m3 occasionally with mesolophid.

The large-sized *Megacricetodon gersii* is characterize by having most of the M1 with an anterocone deeply subdivided, occasionally having a entomesoloph, and short or medium mesoloph in the M1 and M2; the anteroconid of the m1 is simple, slightly subdivided or 8-shaped, ectomesolophid absent, mesolophid in the m1 or m2 short or absent; and occasionally short mesolophid in the m3. *Megacricetodon gersii* occurred in the local zone Dd and E (middle Aragonian) and not in the local zone F (upper Aragonian) as previously thought.

These species have been included in the "*Megacricetodon primitivus* group", together with the species *M. primitivus* and *M. alvarezae*. This group had its first occurrence in France during the MN 4, dispersing through the Iberian Peninsula (Spain and Portugal) at the latest MN 4. Finally, it would reach Central Europe (Switzerland) during MN 5.

6.7. REFERENCES

Abdul Aziz, H., M. Böhme, A. Rocholl, J. Prieto, J. R. Wijbrans, V. Bachtadse, and A. Ulbig. 2010. Integrated stratigraphy and 40Ar/39Ar chronology of the Early to Middle Miocene Upper Freshwater Molasse in western Bavaria (Germany). International Journal of Earth Sciences 99:1859-1886.

Abdul Aziz, H., M. Böhme, A. Rocholl, A. Zwing, J. Prieto, J. R. Wijbrans, K. Heissig, and V. Bachtadse. 2008. Integrated stratigraphy and 40Ar/39Ar chronology of the Early to Middle Miocene Upper Freshwater Molasse in eastern Bavaria (Germany). International Journal of Earth Sciences 97:115-134.

Aguilar, J. 1980. Nouvelle interpretation de l'evolution du genre *Megacricetodon* au cours du Miocene. Paleovertebrata Volumen Jubilaire R. Lavocat:355-366.

Aguilar, J. P. 1995. Evolution de la lignée *Megacricetodon collongensis-Megacricetodon rousillonensis* (Cricetidae, Rodentia, Mammalia) au cours du Miocène inférieur et moyen dans le sud de la France. Palaeovertebrata 24:1-45.

Aguilar, J. P., M. Calvet, and J. Michaux. 1986. Découvertes de faunes de micromammifères dans les Pyrénées Orientales (France) de l'Oligocène supérieur au Miocène supérieur; espèces nouvelles et réflexion sur l'étalonnage des échelles continentale et marine. Comptes Rendus de l'Académie des Sciences de Paris Sér. II, 303(8):755-760.

Agustí, J., P. Anadón, L. Ginsburg, P. Mein, and P. Moissenet. 1988. Araya et Mira: nouveaux gisements de mammifères dans le Miocène inférieur-moyen des chaînes Ibériques orientales et méditerranéennes. Conséquences stratigraphiques et structurales. Paleontologia i Evolucio 22:83-101.

Alcalá, L., A. Alonso-Zarza, M. Álvarez-Sierra, B. Azanza, J. Calvo, J. Cañaveras, J. v. Dam, M. Garcés, W. Krijgsman, A. v. d. Meulen, P. Pélaez-Campomanes, Pérez-González.A, S. Sánchez Moral, R. Sancho, and E. Sanz Rubio. 2000. El registro sedimentario y faunístico de las cuencas de calatayud-daroca y teruel. evolución paleoambiental y paleoclimática durante el neógeno. Revista de la Sociedad Geológica de España 13:323-343.

Álvarez Sierra, M. A., I. García Paredes, and P. Peláez-Campomanes. 2006. Middle Miocene Rodents from the Tarazona Area. Beiträge zur Paläontologie 30:5-13.

Antunes, M., and P. Mein. 1981. vertébrés du miocène moyen de amor (leiria) importnace stratigraphique. Ciencas de ña erra (UNL) 6:169-188.

Baudelot, S. 1972. Etude des Chiroptères, Insectivores et rongeurs du Miocene de Sansan (Gers): In *Thesis University Toulouse, 496:*, pp. 1-364. Toulouse.

Bolliger, T. v. 1997: The current knowledge of the biozonation with small mammals in the upper freshwater molasse in Switzerland, especially the Hörnli-fan. Paper presented at the BiochroM'97, Montpellier, 1997.

Bowdich, T. E. 1821. An Analysis of the Natural Classification of Mamalia for the Use of Students and Travellers. 115 pp. Smith, J., Paris.

Daams, R. 1981. The dental pattern of the Dormice *Dryomys, Myomimus, Microdyromys* and *Peridyromys*. Utrecht micropaleontological bulletins. Special publication. Utrecht 3:1-113.

Daams, R., and M. Freudenthal. 1974. Early Miocene Cricetidae (Rod. Mam.) from Buñol (province of Valencia, Spain). Scripta Geologica 24:1-19.

Daams, R., L. Alcalá, M. A. Alvarez Sierra, B. Azanza, J. A. van Dam, A. J. van der Meulen, J. Morales, M. Nieto, P. Peláez-Campomanes, and D. Soria. 1998. A stratigraphical framework for Miocene (MN4-MN13) continental sediments of central Spain. Comptes Rendus de l'Academie des Sciences, Serie II. Sciences de la Terre et des Planetes 327:625-631.

Daams, R., and M. Freudenthal. 1988a. Cricetidae (Rodentia) from the type-Aragonian; the genus *Megacricetodon*; pp. 39-132 *i*n M. Freudenthal (ed.), Biostratigraphy and paleoecology of the Neogene micromammalian faunas from the Calatayud-Teruel Basin (Spain). Scripta Geologica, Special Issue 1, Leiden.

Daams, R., and M. Freudenthal. 1988b. Synopsis of the Dutch-Spanish collaboration program in the Neogene of the Calatayud-Teruel basin; pp. 3-18 *i*n M. Freudenthal (ed.), Biostratigraphy and paleoecology of the Neogene micromammalian faunas from the Calatayud-Teruel Basin (Spain). Scripta Geologica, Special Issue 1, Leiden.

Daams, R., M. Freudenthal, and M. Alvarez-Sierra. 1987. Ramblian: a new stage for continental deposits of early Miocene age. Geologie en Minjbouw 65:297-308.

Daams, R., M. Freudenthal, and A. Weerd, van de. 1977. Aragonian, a new stage for continental deposits of Miocene age. Newsletters of Stratigraphy 6:42-55.

Daams, R., A. J. van der Meulen, M. A. Álvarez-Sierra, P. Peláez-Campomanes, J. P. Calvo, M. A. Alonso Zarza, and W. Krijgsman. 1999. Stratigraphy and sedimentology of the Aragonian (Early to Middle Miocene) in its type area (North-Central Spain). Newsletters on Stratigraphy 37:103-139.

Fahlbusch, V. 1964. Die Cricetiden (Mam.) der Oberen Süsswasser-Molasse Bayerns. Bayerische Akademie Wissenschaften. Mathematisch-naturwissenschaftliche Klasse. Munchen 118:1-135.

Freudenthal, M. 1963. Entwicklungsstufen der Miozänen Cricetodontinae (Mam. Rod.). In *Mittelspaniens und ihre Stratigraphische Bedeutung*, pp. 107. Ricks University, Utrecht.

Freudenthal, M., and G. Cuenca-Bescos. 1984. Size variation of fossil rodent populations. Scripta Geologica 76:1-28.

García-Moreno, E. 1987. El género *Megacricetodon* (Cricetidae, Rod.) en el Aragoniense y Vallesiense de la Cuenca del Duero. Relaciones filogeneticas. Col-Pa 41:51-106.

Ginsburg, L., and C. Bulot. 2000. Le cadre stratigraphique du site de Sansan. Memoires du Museum National d'Histoire Naturelle, 183:39-67.

Hernandez-Ballarin, V., A. Oliver, I. Garcia-Paredes, and P. Pelaez-Campomanes. 2010. Preliminary Study of the Rodent Fauna of the Miocene Fossil Site of El Canaveral (Madrid, Spain). Cidaris 30.

Hernández-Ballarín, V., A. Oliver, and P. Pelaez-Campomanes. 2011. Revisión de las asociaciones de mamíferos del tránsito Aragoniense medio y superior de la Cuenca de Madrid; pp. 173-182 *in* A. Pérez-García, F. Gascó, J. M. Gasulla, and F. Escaso (eds.), Viajando a Mundos Pretéritos. Ayuntamiento de Morella, Morella (Castellón).

Hernández Fernández, M., J. A. Cárdaba, J. Cuevas-González, O. Fesharaki, M. J. Salesa, B. Corrales, L. Domingo, J. Elez, P. López Guerrero, N. Sala-Burgos, J. Morales, and N. López Martínez. 2006. Los yacimientos de vertebrados del Mioceno medio de Somosaguas (Pozuelo de Alarcón, Madrid): implicaciones paleoambientales y paleoclimáticas. Estudios Geológicos 62:263-294.

Illiger, J. K. W. 1811. Überblick der Säugthiere nach ihrer Vertheilung über die Welttheile.; pp. 39-160 *in* W. d. Gruyter (ed.), Abhandlungen de physikalischen Klasse der Königlich-Preussischen Akademie der Wissenschaften. Realschul-Buchhandlung, Berlin.

Kälin, D. 1997: The mammal zonation of the Upper Marine Molasse of Switzerland reconsidered. A local biozonation of MN2-MN5. Paper presented at the Actes du Congrès BiochromM'97, Mémoires et Travaux de l'E.P.H.E., Institut de Montpellier, 1997.

Kälin, D., and O. Kempf. 2009. High-resolution stratigraphy from the continental record of the Middle Miocene Northern Alpine Foreland Basin of Switzerland. Neues Jahrbuch Fur Geologie Und Palaontologie-Abhandlungen 254:177-235.

Kempf, O., T. Bolliger, D. Kälin, B. Engesser, and A. Matter. 1997. New magnetostratigraphic calibration of Early to Middle Miocene mammal biozones of the North Alpine Foreland Basin. Actes du Congrès BiochroM`97. Mém. Trav. E.P.H.E., Inst. Montpellier 21:547-561.

Lazzari, V., and J. P. Aguilar. 2007. Les *Megacricetodon* du gisement karstique miocène moyen de Blanquatère 1 (Pyrénées-Orientales, Sud de la France): nouvelles espèces, implications biochronologique et phylogénetique. Geobios, 40: 91-111.

Lopez Olmedo, F., J. A. Diaz de Neira, A. Martin Serrano, J. P. Calvo Sorando, J. Morales Romero, and P. Pelaez-Campomanes. 2004. Unidades estratigraficas en el registro sedimentario neogeno del sector occidental de la cuenca de Madrid, Vol. 17 (1-2), pp. 87-101. Sociedad Geologica de España.

Luis, A., and J. M. Hernando. 2000. Los microvertebrados del Mioceno medio de Somosaguas Sur (Pozuelo de Alarcón, Madrid, España). Coloquios de Paleontología 51:87-136.

Maridet, O. 2003. Révision du genre *Democricetodon* (Mammalia, Rodentia, Cricetinae) et dynamique des faunes de rongeurs du Néogène d'Europe occidentale : évolution, paléobiodiversité et paléobiogéographie, pp. 1-253. l'Universite Claude Bernard – Lyon 1, Lyon.

Mein, P. 1958. Les mammifères de la faune sidérolithique du Vieux -Collonges. Nouvelles Archives du Muséum d'Histoire Naturelle de Lyon 5:1-122.

Menéndez Gamella, A., H. Serrano, M. Presumido, J. A. Cárdaba, and O. Fesharaki. 2010. Yacimientos paleontológicos de Húmera (Mioceno medio-Cuenca de Madrid): Datos preliminares en estratigrafía y paleontología. Cidaris 30:187-196.

Murelaga, X., F. J. Perez-Rivares, M. Vazquez-Urbez, and M. C. Zuluaga. 2008. New biostratigraphic and paleoecologic data from the middle Miocene (Aragonian) from the Tarazona de Aragon area (Ebro Basin) Zaragoza Province, Spain. Ameghiniana 45.

Oliver, A. and P. Peláez-Campomanes. 2014. Early Miocene evolution of the genus *Megacricetodon* in Europe and its palaeobiogeographical implications. Acta Palaeontologica Polonica. doi:http://dx.doi.org/10.4202/app.00099.2014.

Oliver, A. and P. Peláez-Campomanes. In press. Evolutionary patterns of early and middle Aragonian (Miocene) of *Megacricetodon* (Rodentia, Mammalia) from Spain. Palaeontographica Abteilung A.

Pérez, A., B. Azanza, G. Cuenca, G. Pardo, and J. Villena. 1985. Nuevos datos estratigráficos y paleontológicos sobre el Terciario del borde meridional de la Depresión del Ebro (provincia de Zaragoza). Estudios Geológicos, 41(5-6):405-411.

Ruiz-Sánchez, F. J., J. L. Lacomba, and C. Santisteban. 1995. Caracterizacion de *Megacricetodon collongensis* (Mam. Rod.) del Aragoniense de la localidad "Quesa 2 " (Quesa, Valencia). Revista española de Paleontologia 10:151-160.

Schaub, S. 1925. Die Hamsterartige Nagetiere des Tertiärs und ihre lebenden Verwandten. Abhandlungen des Schweizerischen paläontologische Gesellschaft. Mémoires de la Société paléontologique suisse 45 (Années1921-25):1-114.

Sesé, C. 2006. Los roedores y lagomorfos del Neógeno de España. Estudios Geológicos 62:429-480.

Valdés, G. G., C. Sese, and H. Astibia. 1986. Micromamíferos (Rodentia y Lagomorpha) del yacimiento del Mioceno medio de Tarazona de Aragón (Depresión del Ebro, provincia de Zaragoza). Estudios geol. 42:41-55.

van Dam, J. A., H. A. Aziz, M. A. A. Sierra, F. J. Hilgen, L. W. V. D. H. Ostende, L. J. Lourens, P. Mein, A. J. van der Meulen, and P. Pelaez-Campomanes. 2006. Long-period astronomical forcing of mammal turnover. Nature 443:687-691.

van der Meulen, A. J., I. Garcia-Paredes, M. A. Alvarez-Sierra, L. W. V. Ostende, K. Hordijk, A. Oliver, P. Lopez-Guerrero, V. Hernandez-Ballarin, and P. Pelaez-Campomanes. 2011. Biostratigraphy or biochronology? Lessons from the Early and Middle Miocene small Mammal Events in Europe. Geobios 44:309-321.

van der Meulen, A. J., I. García-Paredes, M. A. Álvarez-Sierra, L. W. van den Hoek Ostende, K. Hordijk, A. Oliver, and P. Peláez-Campomanes. 2012. Updated Aragonian biostratigraphy: Small Mammal distribution and its implications for the Miocene European Chronology. Geologica Acta 10:159-179.

APPENDIX 6.1

DISTRIBUTION OF CHARACTER STATES

Table 1. Division of the anterocone M1

Localities			N	MV
Sansan		10 (100%)	10	2,00
Las Umbrias 20	4 (18%)	18 (82%)	22	1,82
Las Umbrias 19		13 (100%)	13	2,00
Las Planas 4BA	2 (8%)	22 (92%)	24	1,92
Las Umbrias 14	1 (6%)	15 (94%)	16	1,94
Las Umbrias 18	1 (25%)	3 (75%)	4	1,75
Las Umbrias 17		14 (100%)	14	2,00
Las Umbrias 12		30 (100%)	30	2,00
Las Umbrias 16		22 (100%)	22	2,00
Las Umbrias 11	6 (12%)	46 (88%)	52	1,88
Las Umbrias 10	2 (13%)	14 (88%)	16	1,88
Las Umbrias 9		10 (100%)	10	2,00
Las Umbrias 8	1 (6%)	17 (94%)	18	1,94
Las Umbrias 7	5 (28%)	13 (72%)	18	1,72
Valdemoros 7G		3 (100%)	3	2,00
Valdemoros 7F	2 (13%)	14 (88%)	16	1,88
Valdemoros 7E	4 (18%)	18 (82%)	22	1,82
Las Umbrias 5	1 (17%)	5 (83%)	6	1,83
Los Umbrias 4	4 (29%)	10 (71%)	14	1,71
Valdemoros 7D		4 (100%)	4	2,00
Las Umbrias 3	1 (7%)	13 (93%)	14	1,93
Vargas 11		4 (100%)	4	2,00
Las Umbrias 2	1 (14%)	6 (86%)	7	1,86
Las Umbrias 1		8 (100%)	8	2,00
Valdemoros 3F	1 (6%)	17 (94%)	18	1,94
Valdemoros 3E	4 (10%)	37 (90%)	41	1,90
Valdemoros 7C	6 (20%)	24 (80%)	30	1,80
Valdemoros 7B	1 (4%)	24 (96%)	25	1,96
Valdemoros 1A	2 (9%)	21 (91%)	23	1,91
Valdemoros 7A	4 (20%)	16 (80%)	20	1,80
Valdemoros 8B		3 (100%)	3	2,00
Valdemoros 8C	1 (33%)	2 (67%)	3	1,67
Vargas 8C	6 (14%)	37 (86%)	43	1,86
Vargas 8B	2 (6%)	31 (94%)	33	1,94
Casetón 2B		1 (100%)	1	2,00
Casetón 1A	11 (22%)	39 (78%)	50	1,78
Vargas 7	6 (9%)	58 (91%)	64	1,91
Valdemoros 3D	1 (4%)	23 (96%)	24	1,96

Table 2. Anterior cingulum M1

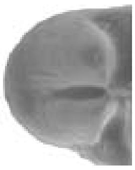
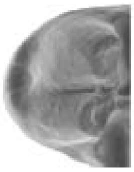
Localities				N	MV
Sansan	1 (10%)	8 (80%)	1 (10%)	10	2,00
Las Umbrias 20	14 (64%)	6 (27%)	2 (9%)	22	1,45
Las Umbrias 19	3 (23%)	6 (46%)	4 (31%)	13	2,08
Las Planas 4BA	4 (17%)	15 (63%)	5 (21%)	24	2,04
Las Umbrias 14	3 (19%)	7 (44%)	6 (38%)	16	2,19
Las Umbrias 18	1 (25%)	2 (50%)	1 (25%)	4	2,00
Las Umbrias 17	4 (29%)	6 (43%)	4 (29%)	14	2,00
Las Umbrias 12	9 (30%)	15 (50%)	6 (20%)	30	1,90
Las Umbrias 16		12 (55%)	10 (45%)	22	2,45
Las Umbrias 11	3 (6%)	35 (67%)	14 (27%)	52	2,21
Las Umbrias 10	2 (13%)	7 (44%)	7 (44%)	16	2,31
Las Umbrias 9	2 (20%)	6 (60%)	2 (20%)	10	2,00
Las Umbrias 8	4 (22%)	10 (56%)	4 (22%)	18	2,00
Las Umbrias 7	8 (44%)	8 (44%)	2 (11%)	18	1,67
Valdemoros 7G		3 (100%)		3	2,00
Valdemoros 7F	2 (13%)	9 (56%)	5 (31%)	16	2,19
Valdemoros 7E	4 (18%)	13 (59%)	5 (23%)	22	2,05
Las Umbrias 5	1 (17%)	2 (33%)	3 (50%)	6	2,33
Los Umbrias 4	5 (36%)	8 (57%)	1 (7%)	14	1,71
Valdemoros 7D	2 (50%)	2 (50%)		4	1,50
Las Umbrias 3	1 (7%)	11 (79%)	2 (14%)	14	2,07
Vargas 11	1 (25%)	2 (50%)	1 (25%)	4	2,00
Las Umbrias 2		5 (71%)	2 (29%)	7	2,29
Las Umbrias 1		6 (75%)	2 (25%)	8	2,25
Valdemoros 3F	1 (6%)	15 (83%)	2 (11%)	18	2,06
Valdemoros 3E	16 (39%)	18 (44%)	7 (17%)	41	1,78
Valdemoros 7C	3 (10%)	24 (80%)	3 (10%)	30	2,00
Valdemoros 7B	1 (4%)	21 (84%)	3 (12%)	25	2,08
Valdemoros 1A	2 (9%)	18 (78%)	3 (13%)	23	2,04
Valdemoros 7A	2 (10%)	18 (90%)		20	1,90
Valdemoros 8B		3 (100%)		3	2,00
Valdemoros 8C	1 (33%)	1 (33%)	1 (33%)	3	2,00
Vargas 8C	8 (19%)	31 (72%)	4 (9%)	43	1,91
Vargas 8B	7 (21%)	24 (73%)	2 (6%)	33	1,85
Casetón 2B		1 (100%)		1	2,00
Casetón 1A	6 (12%)	35 (70%)	9 (18%)	50	2,06
Vargas 7	17 (27%)	46 (72%)	1 (2%)	64	1,75
Valdemoros 3D	7 (29%)	15 (63%)	2 (8%)	24	1,79

Table 3. Symmetry of the Anterocone M1

Localities				N
Sansan	1 (17%)	5 (83%)		6
Las Umbrias 12	7 (20%)	28 (80%)		35
Las Umbrias 16	1 (4%)	25 (96%)		26
Las Umbrias 11	6 (11%)	48 (89%)		54
Las Umbrias 10		16 (100%)		16
Las Umbrias 9	1 (7%)	13 (93%)		14
Las Umbrias 8	3 (16%)	16 (84%)		19
Las Umbrias 7	1 (5%)	19 (95%)		20
Valdemoros 7G	1 (33%)	2 (67%)		3
Valdemoros 7F	2 (12%)	15 (88%)		17
Valdemoros 7E	4 (17%)	19 (83%)		23
Las Umbrias 5	1 (17%)	5 (83%)		6
Los Umbrias 4	1 (7%)	14 (93%)		15
Valdemoros 7D		4 (100%)		4
Las Umbrias 3		15 (100%)		15
Vargas 11	2 (40%)	3 (60%)		5
Las Umbrias 2		6 (100%)		6
Las Umbrias 1		9 (100%)		9
Valdemoros 3F	2 (10%)	19 (90%)		21
Valdemoros 3E	7 (16%)	36 (84%)		43
Valdemoros 7C	4 (12%)	29 (88%)		33
Valdemoros 7B	8 (25%)	24 (75%)		32
Valdemoros 1A	6 (23%)	18 (69%)	2 (8%)	26
Valdemoros 7A	4 (19%)	16 (76%)	1 (5%)	21
Valdemoros 8B	2 (40%)	3 (60%)		5
Valdemoros 8C		6 (100%)		6
Vargas 8C	12 (25%)	35 (73%)	1 (2%)	48
Vargas 8B	10 (25%)	28 (70%)	2 (5%)	40
Casetón 2B	1 (100%)			1
Casetón 1A	5 (9%)	51 (91%)		56
Vargas 7	23 (34%)	44 (65%)	1 (1%)	68
Valdemoros 3D	3 (10%)	25 (86%)	1 (3%)	29

Table 4. Anterolophule M1

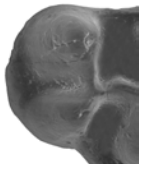
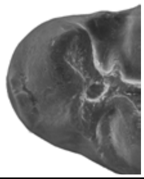
Localities					N
Las Umbrias 12	31 (82%)	6 (16%)	1 (3%)		38
Las Umbrias 16	21 (78%)	6 (22%)			27
Las Umbrias 11	36 (64%)	19 (34%)	1 (2%)		56
Las Umbrias 10	9 (56%)	7 (44%)			16
Las Umbrias 9	10 (67%)	5 (33%)			15
Las Umbrias 8	10 (45%)	12 (55%)			22
Las Umbrias 7	7 (30%)	15 (65%)	1 (4%)		23
Valdemoros 7G	1 (25%)	3 (75%)			4
Valdemoros 7F	12 (71%)	3 (18%)	2 (12%)		17
Valdemoros 7E	17 (68%)	8 (32%)			25
Las Umbrias 5	3 (38%)	5 (63%)			8
Los Umbrias 4	4 (27%)	11 (73%)			15
Valdemoros 7D	2 (33%)	3 (50%)	1 (17%)		6
Las Umbrias 3	9 (56%)	7 (44%)			16
Vargas 11	4 (67%)	2 (33%)			6
Las Umbrias 2	6 (75%)	2 (25%)			8
Las Umbrias 1	2 (22%)	7 (78%)			9
Valdemoros 3F	18 (82%)	4 (18%)			22
Valdemoros 3E	25 (56%)	18 (40%)	2 (4%)		45
Valdemoros 7C	18 (58%)	13 (42%)			31
Valdemoros 7B	18 (53%)	14 (41%)	2 (6%)		34
Valdemoros 1A	14 (50%)	14 (50%)			28
Valdemoros 7A	10 (45%)	11 (50%)	1 (5%)		22
Valdemoros 8B	2 (40%)	3 (60%)			5
Valdemoros 8C	1 (17%)	5 (83%)			6
Vargas 8C	27 (54%)	22 (44%)	1 (2%)		50
Vargas 8B	21 (48%)	23 (52%)			44
Casetón 2B	1 (100%)				1
Casetón 1A	29 (50%)	27 (47%)	2 (3%)		58
Vargas 7	24 (33%)	47 (65%)	1 (1%)		72
Valdemoros 3D	15 (44%)	17 (50%)	1 (3%)	1 (5%)	34

Table 5. Labial Spur of the Anterolophule M1

Localities							N
Sansan	1	(10%)	1	(10%)	8	(80%)	10
Las Umbrias 20	5	(15%)	2	(6%)	27	(79%)	34
Las Umbrias 19	3	(11%)			25	(89%)	28
Las Planas 4BA	4	(12%)	2	(6%)	28	(82%)	34
Las Umbrias 14	2	(11%)	2	(11%)	14	(78%)	18
Las Umbrias 18	1	(13%)			7	(88%)	8
Las Umbrias 17	1	(6%)	1	(6%)	15	(88%)	17
Las Umbrias 12	5	(12%)	4	(10%)	33	(79%)	42
Las Umbrias 16	3	(9%)	2	(6%)	30	(86%)	35
Las Umbrias 11	7	(10%)	6	(9%)	54	(81%)	67
Las Umbrias 10					17	(100%)	17
Las Umbrias 9	4	(25%)			12	(75%)	16
Las Umbrias 8	1	(4%)	4	(16%)	20	(80%)	25
Las Umbrias 7	3	(13%)	4	(17%)	16	(70%)	23
Valdemoros 7G					4	(100%)	4
Valdemoros 7F	7	(39%)	2	(11%)	9	(50%)	18
Valdemoros 7E	4	(15%)	3	(12%)	19	(73%)	26
Las Umbrias 5	1	(11%)	2	(22%)	6	(67%)	9
Los Umbrias 4	5	(28%)	3	(17%)	10	(56%)	18
Valdemoros 7D	1	(14%)	1	(14%)	5	(71%)	7
Las Umbrias 3	4	(25%)	3	(19%)	9	(56%)	16
Vargas 11	2	(33%)			4	(67%)	6
Las Umbrias 2	3	(30%)	1	(10%)	6	(60%)	10
Las Umbrias 1	1	(9%)	1	(9%)	9	(82%)	11
Valdemoros 3F	6	(23%)	3	(12%)	17	(65%)	26
Valdemoros 3E	8	(15%)	5	(10%)	39	(75%)	52
Valdemoros 7C	2	(5%)	4	(11%)	32	(84%)	38
Valdemoros 7B	3	(8%)	3	(8%)	30	(83%)	36
Valdemoros 1A	5	(18%)	2	(7%)	21	(75%)	28
Valdemoros 7A	3	(14%)	1	(5%)	18	(82%)	22
Valdemoros 8B					6	(100%)	6
Valdemoros 8C	1	(17%)	2	(33%)	3	(50%)	6
Vargas 8C	19	(35%)	3	(5%)	33	(60%)	55
Vargas 8B	8	(15%)	3	(6%)	43	(80%)	54
Casetón 2B					1	(100%)	1
Casetón 1A	11	(19%)	8	(14%)	38	(67%)	57
Vargas 7	22	(28%)	13	(16%)	44	(56%)	79
Valdemoros 3D	20	(49%)	1	(2%)	20	(49%)	41

Table 6. Protolophule of the M1

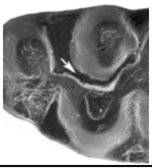
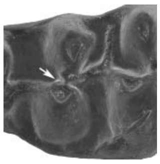
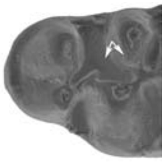
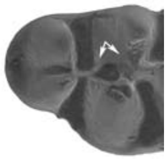
Localities											N
Sansan					10	(100%)					10
Las Umbrias 20					24	(75%)	4	(13%)	4	(13%)	32
Las Umbrias 19					23	(92%)			2	(8%)	25
Las Planas 4BA					31	(89%)	2	(6%)	2	(6%)	35
Las Umbrias 14					16	(100%)					16
Las Umbrias 18					7	(88%)			1	(13%)	8
Las Umbrias 17					14	(93%)			1	(7%)	15
Las Umbrias 12					36	(92%)	2	(5%)	1	(3%)	39
Las Umbrias 16					33	(92%)	1	(3%)	2	(6%)	36
Las Umbrias 11					61	(91%)	2	(3%)	4	(6%)	67
Las Umbrias 10					16	(100%)					16
Las Umbrias 9					12	(75%)	2	(13%)	2	(13%)	16
Las Umbrias 8			1	(4%)	21	(84%)			3	(12%)	25
Las Umbrias 7					16	(76%)	2	(10%)	3	(14%)	21
Valdemoros 7G					4	(100%)					4
Valdemoros 7F					13	(72%)			5	(28%)	18
Valdemoros 7E					23	(88%)	1	(4%)	2	(8%)	26
Las Umbrias 5					8	(89%)	1	(11%)			9
Los Umbrias 4					14	(78%)	2	(11%)	2	(11%)	18
Valdemoros 7D					7	(100%)					7
Las Umbrias 3					14	(88%)	1	(6%)	1	(6%)	16
Vargas 11					5	(83%)	1	(17%)			6
Las Umbrias 2					7	(88%)			1	(13%)	8
Las Umbrias 1					8	(89%)			1	(11%)	9
Valdemoros 3F					24	(96%)	1	(4%)			25
Valdemoros 3E					48	(94%)	2	(4%)	1	(2%)	51
Valdemoros 7C					34	(97%)			1	(3%)	35
Valdemoros 7B					30	(94%)	2	(6%)			32
Valdemoros 1A					24	(86%)	2	(7%)	2	(7%)	28
Valdemoros 7A	1	(5%)			16	(84%)	1	(5%)	1	(5%)	19
Valdemoros 8B					6	(100%)					6
Valdemoros 8C					4	(80%)	1	(20%)			5
Vargas 8C					43	(78%)	10	(18%)	2	(4%)	55
Vargas 8B					50	(91%)	3	(5%)	2	(4%)	55
Casetón 2B					1	(100%)					1
Casetón 1A					57	(98%)			1		58
Vargas 7					59	(76%)	13	(17%)	6	(8%)	78
Valdemoros 3D					30	(75%)	5	(13%)	5	(13%)	40

Table 7. Ectoloph M1

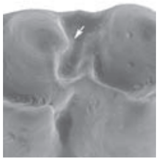
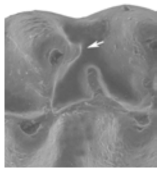
Localities							N	MV
Sansan	2	(18%)	9	(82%)			11	1,82
Las Umbrias 20	9	(27%)	12	(36%)	12	(36%)	33	2,09
Las Umbrias 19	5	(17%)	17	(57%)	8	(27%)	30	2,10
Las Planas 4BA	6	(17%)	20	(57%)	9	(26%)	35	2,09
Las Umbrias 14			11	(55%)	9	(45%)	20	2,45
Las Umbrias 18	3	(38%)	4	(50%)	1	(13%)	8	1,75
Las Umbrias 17	2	(13%)	5	(31%)	9	(56%)	16	2,44
Las Umbrias 12	1	(3%)	13	(33%)	26	(65%)	40	2,63
Las Umbrias 16	4	(11%)	12	(34%)	19	(54%)	35	2,43
Las Umbrias 11	8	(12%)	31	(47%)	27	(41%)	66	2,29
Las Umbrias 10	3	(18%)	10	(59%)	4	(24%)	17	2,06
Las Umbrias 9	3	(21%)	9	(64%)	2	(14%)	14	1,93
Las Umbrias 8	1	(4%)	17	(65%)	8	(31%)	26	2,27
Las Umbrias 7	4	(21%)	10	(53%)	5	(26%)	19	2,05
Valdemoros 7G			3	(60%)	2	(40%)	5	2,40
Valdemoros 7F	1	(6%)	11	(69%)	4	(25%)	16	2,19
Valdemoros 7E	3	(12%)	18	(69%)	5	(19%)	26	2,08
Las Umbrias 5			6	(67%)	3	(33%)	9	2,33
Los Umbrias 4	4	(21%)	9	(47%)	6	(32%)	19	2,11
Valdemoros 7D			5	(71%)	2	(29%)	7	2,29
Las Umbrias 3	1	(6%)	11	(69%)	4	(25%)	16	2,19
Vargas 11	2	(33%)	1	(17%)	3	(50%)	6	2,17
Las Umbrias 2			6	(75%)	2	(25%)	8	2,25
Las Umbrias 1			8	(73%)	3	(27%)	11	2,27
Valdemoros 3F	11	(42%)	12	(46%)	3	(12%)	26	1,69
Valdemoros 3E	12	(22%)	32	(58%)	11	(20%)	55	1,98
Valdemoros 7C	6	(17%)	22	(61%)	8	(22%)	36	2,06
Valdemoros 7B	7	(20%)	19	(54%)	9	(26%)	35	2,06
Valdemoros 1A	2	(7%)	19	(68%)	7	(25%)	28	2,18
Valdemoros 7A	3	(14%)	12	(55%)	7	(32%)	22	2,18
Valdemoros 8B	1	(20%)	2	(40%)	2	(40%)	5	2,20
Valdemoros 8C	1	(17%)	3	(50%)	2	(33%)	6	2,17
Vargas 8C	10	(19%)	32	(59%)	12	(22%)	54	2,04
Vargas 8B	13	(23%)	35	(61%)	9	(16%)	57	1,93
Casetón 2B			1	(100%)			1	2,00
Casetón 1A	13	(22%)	36	(62%)	9	(16%)	58	1,93
Vargas 7	13	(15%)	64	(76%)	7	(8%)	84	1,93
Valdemoros 3D	12	(27%)	32	(71%)	1	(2%)	45	1,76

Table 8. Mesoloph M1

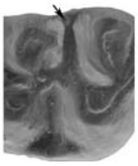
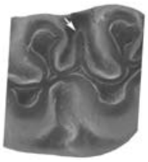
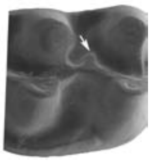
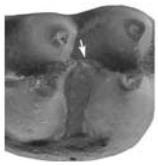
Localities									N	MV
Sansan			1	(9%)	10	(91%)			11	2,91
Las Umbrias 20	3	(9%)	12	(34%)	19	(54%)	1	(3%)	35	2,51
Las Umbrias 19			9	(30%)	21	(70%)			30	2,70
Las Planas 4BA			8	(23%)	26	(74%)	1	(3%)	35	2,80
Las Umbrias 14			5	(24%)	16	(76%)			21	2,76
Las Umbrias 18					8	(100%)			8	3,00
Las Umbrias 17			4	(25%)	12	(75%)			16	2,75
Las Umbrias 12			9	(23%)	30	(75%)	1	(3%)	40	2,80
Las Umbrias 16	1	(3%)	7	(20%)	26	(74%)	1	(3%)	35	2,77
Las Umbrias 11	1	(2%)	17	(26%)	47	(71%)	1	(2%)	66	2,73
Las Umbrias 10			1	(6%)	15	(88%)	1	(6%)	17	3,00
Las Umbrias 9			3	(20%)	12	(80%)			15	2,80
Las Umbrias 8			5	(19%)	21	(81%)			26	2,81
Las Umbrias 7			5	(25%)	15	(75%)			20	2,75
Valdemoros 7G	1	(20%)	1	(20%)	3	(60%)			5	2,40
Valdemoros 7F			4	(24%)	13	(76%)			17	2,76
Valdemoros 7E			5	(19%)	20	(77%)	1	(4%)	26	2,85
Las Umbrias 5	1	(11%)	1	(11%)	7	(78%)			9	2,67
Los Umbrias 4	1	(5%)	10	(50%)	8	(40%)	1	(5%)	20	2,45
Valdemoros 7D			1	(14%)	6	(86%)			7	2,86
Las Umbrias 3	2	(12%)	5	(29%)	10	(59%)			17	2,47
Vargas 11			2	(33%)	4	(67%)			6	2,67
Las Umbrias 2	1	(14%)	4	(57%)	2	(29%)			7	2,14
Las Umbrias 1			8	(67%)	4	(33%)			12	2,33
Valdemoros 3F	2	(8%)	14	(54%)	10	(38%)			26	2,31
Valdemoros 3E	1	(2%)	21	(40%)	30	(58%)			52	2,56
Valdemoros 7C			8	(23%)	27	(77%)			35	2,77
Valdemoros 7B			12	(34%)	22	(63%)	1	(3%)	35	2,69
Valdemoros 1A			10	(37%)	16	(59%)	1	(4%)	27	2,67
Valdemoros 7A			8	(36%)	14	(64%)			22	2,64
Valdemoros 8B			3	(50%)	2	(33%)	1	(17%)	6	2,67
Valdemoros 8C			1	(17%)	4	(67%)	1	(17%)	6	3,00
Vargas 8C			41	(72%)	16	(28%)			57	2,28
Vargas 8B	5	(9%)	30	(53%)	22	(39%)			57	2,30
Casetón 2B					1	(100%)			1	3,00
Casetón 1A	4	(7%)	36	(59%)	19	(31%)	2	(3%)	61	2,31
Vargas 7	4	(5%)	48	(56%)	33	(39%)			85	2,34
Valdemoros 3D	1	(2%)	21	(48%)	22	(50%)			44	2,48

Table 9. Lingual mesocingulum of the M1.

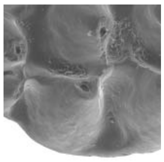
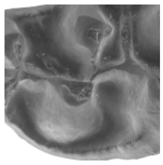
Localities			N
Las Umbrias 12	35 (88%)	5 (13%)	40
Las Umbrias 16	31 (91%)	3 (9%)	34
Las Umbrias 11	55 (87%)	8 (13%)	63
Las Umbrias 10	14 (82%)	3 (18%)	17
Las Umbrias 9	11 (85%)	2 (15%)	13
Las Umbrias 8	22 (85%)	4 (15%)	26
Las Umbrias 7	18 (90%)	2 (10%)	20
Valdemoros 7G	3 (60%)	2 (40%)	5
Valdemoros 7F	9 (60%)	6 (40%)	15
Valdemoros 7E	19 (73%)	7 (27%)	26
Las Umbrias 5	2 (29%)	5 (71%)	7
Los Umbrias 4	14 (78%)	4 (22%)	18
Valdemoros 7D	7 (100%)		7
Las Umbrias 3	12 (71%)	5 (29%)	17
Vargas 11	4 (67%)	2 (33%)	6
Las Umbrias 2	7 (78%)	2 (22%)	9
Las Umbrias 1	4 (36%)	7 (64%)	11
Valdemoros 3F	21 (84%)	4 (16%)	25
Valdemoros 3E	47 (89%)	6 (11%)	53
Valdemoros 7C	25 (66%)	13 (34%)	38
Valdemoros 7B	21 (68%)	10 (32%)	31
Valdemoros 1A	17 (65%)	9 (35%)	26
Valdemoros 7A	15 (68%)	7 (32%)	22
Valdemoros 8B	2 (40%)	3 (60%)	5
Valdemoros 8C	6 (100%)		6
Vargas 8C	40 (74%)	14 (26%)	54
Vargas 8B	41 (79%)	11 (21%)	52
Casetón 2B		1 (100%)	1
Casetón 1A	46 (79%)	12 (21%)	58
Vargas 7	61 (72%)	24 (28%)	85
Valdemoros 3D	32 (80%)	8 (20%)	40

Table 10. Connection Mesoloph-Ectoloph M1

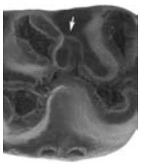
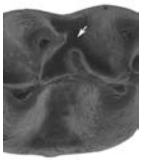
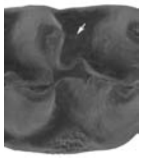
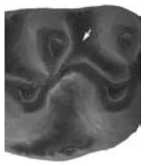
Localities					N
Sansan	1 (17%)	4 (67%)	1 (17%)		6
Las Umbrias 20	5 (15%)	20 (61%)	8 (24%)		33
Las Umbrias 19	4 (13%)	21 (70%)	5 (17%)		30
Las Planas 4BA	11 (31%)	18 (51%)	5 (14%)	1 (3%)	35
Las Umbrias 14	8 (42%)	11 (58%)			19
Las Umbrias 18	2 (25%)	3 (38%)	3 (38%)		8
Las Umbrias 17	4 (25%)	10 (63%)	2 (13%)		16
Las Umbrias 12	14 (36%)	23 (59%)	1 (3%)	1 (3%)	39
Las Umbrias 16	13 (38%)	15 (44%)	4 (12%)	2 (6%)	34
Las Umbrias 11	27 (42%)	31 (48%)	6 (9%)	1 (2%)	65
Las Umbrias 10	3 (18%)	11 (65%)	3 (18%)		17
Las Umbrias 9	4 (31%)	9 (69%)			13
Las Umbrias 8	9 (35%)	16 (62%)	1 (4%)		26
Las Umbrias 7	5 (26%)	10 (53%)	4 (21%)		19
Valdemoros 7G	2 (40%)	3 (60%)			5
Valdemoros 7F	5 (31%)	10 (63%)	1 (6%)		16
Valdemoros 7E	7 (27%)	16 (62%)	2 (8%)	1 (4%)	26
Las Umbrias 5	4 (44%)	5 (56%)			9
Los Umbrias 4	5 (26%)	11 (58%)	2 (11%)	1 (5%)	19
Valdemoros 7D	2 (29%)	5 (71%)			7
Las Umbrias 3	8 (47%)	8 (47%)	1 (6%)		17
Vargas 11	2 (33%)	3 (50%)	1 (17%)		6
Las Umbrias 2	1 (14%)	6 (86%)			7
Las Umbrias 1	1 (9%)	10 (91%)			11
Valdemoros 3F	1 (4%)	15 (60%)	9 (36%)		25
Valdemoros 3E	4 (8%)	37 (71%)	11 (21%)		52
Valdemoros 7C	3 (9%)	26 (76%)	5 (15%)		34
Valdemoros 7B	6 (17%)	22 (63%)	6 (17%)	1 (3%)	35
Valdemoros 1A	3 (11%)	21 (78%)	2 (7%)	1 (4%)	27
Valdemoros 7A	1 (5%)	18 (82%)	3 (14%)		22
Valdemoros 8B	1 (20%)	2 (40%)	1 (20%)	1 (20%)	5
Valdemoros 8C		4 (67%)	1 (17%)	1 (17%)	6
Vargas 8C	3 (6%)	42 (78%)	9 (17%)		54
Vargas 8B	6 (11%)	39 (68%)	12 (21%)		57
Casetón 2B		1 (100%)			1
Casetón 1A	2 (4%)	43 (78%)	8 (15%)	2 (4%)	55
Vargas 7	8 (10%)	64 (77%)	11 (13%)		83
Valdemoros 3D	4 (9%)	27 (63%)	12 (28%)		43

Table 11. Entomesoloph M1

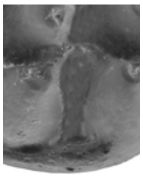
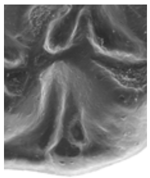
Localities			N
Sansan	11 (100%)		11
Las Umbrias 20	29 (91%)	3 (9%)	32
Las Umbrias 19	24 (96%)	1 (4%)	25
Las Planas 4BA	31 (94%)	2 (6%)	33
Las Umbrias 14	19 (95%)	1 (5%)	20
Las Umbrias 18	9 (100%)		9
Las Umbrias 17	16 (100%)		16
Las Umbrias 12	37 (93%)	3 (8%)	40
Las Umbrias 16	31 (97%)	1 (3%)	32
Las Umbrias 11	58 (98%)	1 (2%)	59
Las Umbrias 10	16 (94%)	1 (6%)	17
Las Umbrias 9	11 (100%)		11
Las Umbrias 8	26 (100%)		26
Las Umbrias 7	17 (85%)	3 (15%)	20
Valdemoros 7G	5 (100%)		5
Valdemoros 7F	15 (100%)		15
Valdemoros 7E	25 (96%)	1 (4%)	26
Las Umbrias 5	3 (50%)	3 (50%)	6
Los Umbrias 4	17 (100%)		17
Valdemoros 7D	7 (100%)		7
Las Umbrias 3	17 (100%)		17
Vargas 11	6 (100%)		6
Las Umbrias 2	8 (100%)		8
Las Umbrias 1	11 (100%)		11
Valdemoros 3F	20 (77%)	6 (23%)	26
Valdemoros 3E	47 (92%)	4 (8%)	51
Valdemoros 7C	35 (97%)	1 (3%)	36
Valdemoros 7B	29 (100%)		29
Valdemoros 1A	26 (96%)	1 (4%)	27
Valdemoros 7A	21 (100%)		21
Valdemoros 8B	5 (100%)		5
Valdemoros 8C	6 (100%)		6
Vargas 8C	44 (83%)	9 (17%)	53
Vargas 8B	41 (77%)	12 (23%)	53
Casetón 2B	1 (100%)		1
Casetón 1A	56 (89%)	7 (11%)	63
Vargas 7	77 (95%)	4 (5%)	81
Valdemoros 3D	33 (94%)	2 (6%)	35

Table 12. Metalophule M1

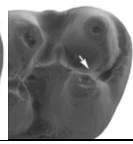
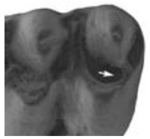
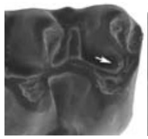
Localities									N
Sansan				5 (56%)	4 (44%)				9
Las Umbrias 20				4 (14%)	23 (79%)	1 (3%)		1 (3%)	29
Las Umbrias 19	1 (4%)	1 (4%)		3 (13%)	17 (74%)			1 (4%)	23
Las Planas 4BA			2 (8%)	2 (8%)	21 (81%)		1 (4%)		26
Las Umbrias 14		1 (6%)			15 (94%)				16
Las Umbrias 18	1 (14%)				5 (71%)	1 (14%)			7
Las Umbrias 17	1 (8%)			1 (8%)	9 (75%)	1 (8%)			12
Las Umbrias 12				4 (12%)	27 (79%)	2 (6%)		1 (3%)	34
Las Umbrias 16		1 (3%)	1 (3%)		31 (94%)				33
Las Umbrias 11		1 (2%)	5 (8%)	7 (12%)	43 (73%)		1 (2%)	2 (3%)	59
Las Umbrias 10					15 (100%)				15
Las Umbrias 9				2 (15%)	11 (85%)				13
Las Umbrias 8				1 (5%)	20 (91%)		1 (5%)		22
Las Umbrias 7					17 (94%)			1 (6%)	18
Valdemoros 7G				1 (25%)	3 (75%)				4
Valdemoros 7F				2 (13%)	11 (69%)			3 (19%)	16
Valdemoros 7E			2 (8%)	2 (8%)	20 (83%)				24
Las Umbrias 5					9 (100%)				9
Los Umbrias 4			1 (6%)	4 (24%)	12 (71%)				17
Valdemoros 7D			1 (17%)	1 (17%)	4 (67%)				6
Las Umbrias 3					14 (88%)	1 (6%)		1 (6%)	16
Vargas 11					2 (67%)	1 (33%)			3
Las Umbrias 2				1 (13%)	6 (75%)		1 (13%)		8
Las Umbrias 1					9 (100%)				9
Valdemoros 3F			1 (4%)	2 (9%)	20 (87%)				23
Valdemoros 3E	1 (2%)			1 (2%)	45 (92%)	2 (4%)			49
Valdemoros 7C	1 (3%)			1 (3%)	28 (93%)				30
Valdemoros 7B			1 (4%)	1 (4%)	25 (89%)	1 (4%)			28
Valdemoros 1A				3 (13%)	19 (79%)	2 (8%)			24
Valdemoros 7A				3 (19%)	13 (81%)				16
Valdemoros 8B		1 (25%)			2 (50%)	1 (25%)			4
Valdemoros 8C			2 (40%)		3 (60%)				5
Vargas 8C	1 (2%)			1 (2%)	50 (91%)	2 (4%)	1 (2%)		55
Vargas 8B		2 (4%)		7 (13%)	43 (80%)	1 (2%)		1 (2%)	54
Casetón 2B							1 (100%)		1
Casetón 1A		1 (2%)	1 (2%)	4 (7%)	50 (89%)				56
Vargas 7		1 (1%)	2 (3%)	5 (7%)	57 (79%)	6 (8%)	1 (1%)		72
Valdemoros 3D		1 (3%)	1 (3%)		31 (91%)			1 (3%)	34

Table 13. Protolophule M2

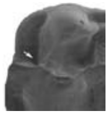
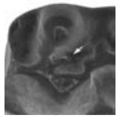
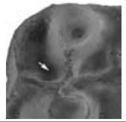
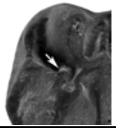
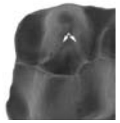
Localities										N
Sansan	3 (60%)						2 (40%)			5
Las Umbrias 20	8 (36%)	5 (23%)	3 (14%)	1 (5%)			5 (23%)			22
Las Umbrias 19	5 (36%)	2 (14%)		1 (7%)			6 (43%)			14
Las Planas 4BA	13 (48%)	1 (4%)		1 (4%)	2 (7%)		10 (37%)			27
Las Umbrias 14	12 (67%)	1 (6%)			1 (6%)		4 (22%)			18
Las Umbrias 18	1 (14%)	3 (43%)			1 (14%)		2 (29%)			7
Las Umbrias 17	8 (57%)						6 (43%)			14
Las Umbrias 12	16 (57%)	5 (18%)		2 (7%)	2 (7%)		3 (11%)			28
Las Umbrias 16	10 (29%)	6 (17%)	1 (3%)		8 (23%)		10 (29%)			35
Las Umbrias 11	23 (36%)	5 (8%)	1 (2%)	1 (2%)	12 (19%)		21 (33%)		1 (2%)	64
Las Umbrias 10	3 (33%)	1 (11%)			1 (11%)		4 (44%)			9
Las Umbrias 9	3 (33%)		1 (11%)		2 (22%)		3 (33%)			9
Las Umbrias 8	5 (23%)	2 (9%)			7 (32%)		8 (36%)			22
Las Umbrias 7	15 (68%)	1 (5%)			2 (9%)	1 (5%)	3 (14%)			22
Valdemoros 7G	1 (33%)						2 (67%)			3
Valdemoros 7F	8 (50%)	1 (6%)			1 (6%)		6 (38%)			16
Valdemoros 7E	8 (44%)	2 (11%)				1 (6%)	6 (33%)		1 (6%)	18
Las Umbrias 5	2 (33%)						4 (67%)			6
Los Umbrias 4	6 (26%)	4 (17%)	1 (4%)		1 (4%)		11 (48%)			23
Valdemoros 7D		1 (9%)			1 (9%)		9 (82%)			11
Las Umbrias 3	8 (53%)	3 (20%)					4 (27%)			15
Vargas 11	5 (50%)	3 (30%)					2 (20%)			10
Las Umbrias 2	1 (17%)						5 (83%)			6
Las Umbrias 1	6 (50%)	2 (17%)					3 (25%)		1 (8%)	12
Valdemoros 3F	14 (52%)	9 (33%)					4 (15%)			27
Valdemoros 3E	27 (66%)	10 (24%)			1 (2%)		3 (7%)			41
Valdemoros 7C	11 (52%)	2 (10%)	2 (10%)				6 (29%)			21
Valdemoros 7B	14 (61%)	3 (13%)	1 (4%)		1 (4%)		4 (17%)			23
Valdemoros 1A	6 (46%)				1 (8%)	1 (8%)	5 (38%)			13
Valdemoros 7A	1 (13%)	2 (25%)	1 (13%)		1 (13%)		3 (38%)			8
Valdemoros 8B	3 (38%)	1 (13%)			1 (13%)		3 (38%)			8
Valdemoros 8C	4 (50%)	1 (13%)					3 (38%)			8
Vargas 8C	23 (49%)	19 (40%)	1 (2%)				3 (6%)	1 (2%)		47
Vargas 8B	26 (46%)	27 (47%)					4 (7%)			57
Casetón 2B	3 (60%)	1 (20%)			1 (20%)					5
Casetón 1A	35 (49%)	26 (36%)					11 (15%)			72
Vargas 7	40 (53%)	26 (35%)		2 (3%)			7 (9%)			75
Valdemoros 3D	14 (39%)	13 (36%)					9 (25%)			36

Table 14. Protolophule M2 bis

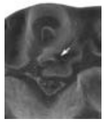
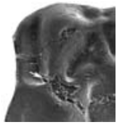
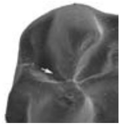
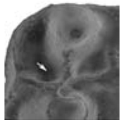
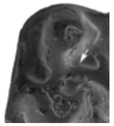
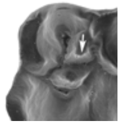
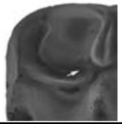
Localities												N
Sansan	3 (60%)						2 (40%)					5
Las Umbrias 20	8 (36%)	5 (23%)	3 (14%)	1 (5%)			4 (18%)		1 (5%)			22
Las Umbrias 19	5 (36%)	2 (14%)		1 (7%)			3 (21%)		3 (21%)			14
Las Planas 4BA	13 (48%)	1 (4%)		1 (4%)	2 (7%)		7 (26%)		3 (11%)			27
Las Umbrias 14	12 (67%)	1 (6%)			1 (6%)		3 (17%)		1 (6%)			18
Las Umbrias 18	1 (14%)	3 (43%)			1 (14%)		2 (29%)					7
Las Umbrias 17	8 (57%)						4 (29%)		2 (14%)			14
Las Umbrias 12	16 (57%)	5 (18%)		2 (7%)	2 (7%)		1 (4%)		2 (7%)			28
Las Umbrias 16	10 (29%)	6 (17%)	1 (3%)		8 (23%)		9 (26%)		1 (3%)			35
Las Umbrias 11	23 (36%)	5 (8%)	1 (2%)	1 (2%)	12 (19%)		15 (23%)		6 (9%)		1 (2%)	64
Las Umbrias 10	3 (33%)	1 (11%)			1 (11%)		3 (33%)		1 (11%)			9
Las Umbrias 9	3 (33%)		1 (11%)		2 (22%)		2 (22%)		1 (11%)			9
Las Umbrias 8	5 (23%)	2 (9%)			7 (32%)		1 (5%)		7 (32%)			22
Las Umbrias 7	15 (68%)	1 (5%)			2 (9%)	1 (5%)	2 (9%)		1 (5%)			22
Valdemoros 7G	1 (33%)						2 (67%)					3
Valdemoros 7F	8 (50%)	1 (6%)			1 (6%)		5 (31%)		1 (6%)			16
Valdemoros 7E	8 (44%)	2 (11%)				1 (6%)	2 (11%)		4 (22%)		1 (6%)	18
Las Umbrias 5	2 (33%)						2 (33%)		2 (33%)			6
Los Umbrias 4	6 (26%)	4 (17%)	1 (4%)		1 (5%)		5 (22%)	1 (4%)	5 (22%)			23
Valdemoros 7D		1 (9%)			1 (9%)		6 (55%)		3 (27%)			11
Las Umbrias 3	8 (50%)	3 (19%)					1 (6%)		4 (25%)			16
Vargas 11	5 (50%)	3 (30%)					2 (20%)					10
Las Umbrias 2	1 (17%)						3 (50%)		2 (33%)			6
Las Umbrias 1	6 (50%)	2 (17%)					3 (25%)				1 (8%)	12
Valdemoros 3F	14 (52%)	9 (33%)					3 (11%)		1 (4%)			27
Valdemoros 3E	27 (66%)	10 (24%)			1 (2%)		3 (7%)					41
Valdemoros 7C	11 (52%)	2 (10%)	2 (10%)				6 (29%)					21
Valdemoros 7B	14 (61%)	3 (13%)	1 (4%)		1 (4%)		2 (9%)		2 (9%)			23
Valdemoros 1A	6 (46%)				1 (8%)	1 (8%)	5 (38%)					13
Valdemoros 7A	1 (13%)	2 (25%)	1 (13%)		1 (13%)		3 (38%)					8
Valdemoros 8B	3 (38%)	1 (13%)			1 (13%)		3 (38%)					8
Valdemoros 8C	4 (50%)	1 (13%)					3 (38%)					8
Vargas 8C	23 (49%)	19 (40%)	1 (2%)				3 (6%)			1 (2%)		47
Vargas 8B	26 (46%)	27 (47%)					4 (7%)					57
Casetón 2B	3 (60%)	1 (20%)			1 (20%)							5
Casetón 1A	35 (49%)	26 (36%)					11 (15%)					72
Vargas 7	40 (53%)	26 (35%)		2 (3%)			7 (9%)					75
Valdemoros 3D	14 (39%)	13 (36%)					9 (25%)					36

Table 15. Anterior Protolophule M2

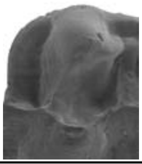
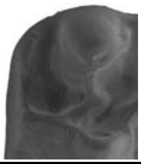
Localities				N
Sansan	3 (100%)			3
Las Umbrias 20	13 (100%)			13
Las Umbrias 19	4 (67%)		3 (33%)	7
Las Planas 4BA	14 (100%)			14
Las Umbrias 14	13 (100%)			13
Las Umbrias 18	4 (100%)			4
Las Umbrias 17	8 (100%)			8
Las Umbrias 12	20 (95%)	1 (5%)		21
Las Umbrias 16	16 (100%)			16
Las Umbrias 11	24 (86%)	4 (14%)		28
Las Umbrias 10	1 (100%)			1
Las Umbrias 9	3 (100%)			3
Las Umbrias 8	7 (100%)			7
Las Umbrias 7	16 (100%)			16
Valdemoros 7G	1 (100%)			1
Valdemoros 7F	9 (100%)			9
Valdemoros 7E	9 (90%)	1 (10%)		10
Las Umbrias 5	2 (100%)			2
Los Umbrias 4	9 (90%)	1 (10%)		10
Valdemoros 7D	1 (100%)			1
Las Umbrias 3	10 (91%)	1 (9%)		11
Vargas 11	6 (75%)	2 (25%)		8
Las Umbrias 2	1 (100%)			1
Las Umbrias 1	7 (88%)	1 (13%)		8
Valdemoros 3F	21 (91%)	2 (9%)		23
Valdemoros 3E	35 (95%)	2 (5%)		37
Valdemoros 7C	13 (100%)			13
Valdemoros 7B	16 (94%)	1 (6%)		17
Valdemoros 1A	6 (100%)			6
Valdemoros 7A	3 (100%)			3
Valdemoros 8B	4 (100%)			4
Valdemoros 8C	5 (100%)			5
Vargas 8C	41 (98%)	1 (2%)		42
Vargas 8B	52 (98%)		1 (2%)	53
Casetón 2B	4 (100%)			4
Casetón 1A	60 (98%)	1 (2%)		61
Vargas 7	66 (100%)			66
Valdemoros 3D	27 (100%)			27

Table 16. Ectoloph M2

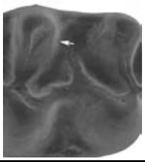
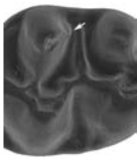
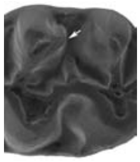
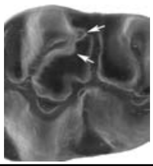
Localities					N	MV
Sansan		5 (63%)	3 (38%)		8	2,38
Las Umbrias 20	4 (14%)	6 (21%)	18 (64%)		28	2,50
Las Umbrias 19		3 (20%)	12 (80%)		15	2,80
Las Planas 4BA		12 (34%)	23 (66%)		35	2,66
Las Umbrias 14		13 (68%)	6 (32%)		19	2,32
Las Umbrias 18		4 (50%)	4 (50%)		8	2,50
Las Umbrias 17		10 (63%)	6 (38%)		16	2,38
Las Umbrias 12		4 (12%)	29 (85%)	1 (3%)	34	2,91
Las Umbrias 16		3 (9%)	32 (91%)		35	2,91
Las Umbrias 11		19 (28%)	49 (72%)		68	2,72
Las Umbrias 10		4 (36%)	7 (64%)		11	2,64
Las Umbrias 9		6 (60%)	4 (40%)		10	2,40
Las Umbrias 8		8 (33%)	16 (67%)		24	2,67
Las Umbrias 7		9 (41%)	13 (59%)		22	2,59
Valdemoros 7G		2 (50%)	2 (50%)		4	2,50
Valdemoros 7F		7 (39%)	11 (61%)		18	2,61
Valdemoros 7E		7 (37%)	12 (63%)		19	2,63
Las Umbrias 5		2 (33%)	4 (67%)		6	2,67
Los Umbrias 4		9 (38%)	15 (63%)		24	2,63
Valdemoros 7D	2 (15%)	6 (46%)	5 (38%)		13	2,23
Las Umbrias 3		6 (40%)	9 (60%)		15	2,60
Vargas 11		2 (20%)	8 (80%)		10	2,80
Las Umbrias 2		1 (17%)	5 (83%)		6	2,83
Las Umbrias 1		4 (33%)	5 (42%)	3 (25%)	12	2,92
Valdemoros 3F	1 (3%)	13 (43%)	15 (50%)	1 (3%)	30	2,53
Valdemoros 3E	1 (3%)	15 (38%)	24 (60%)		40	2,58
Valdemoros 7C	1 (3%)	19 (66%)	9 (31%)		29	2,28
Valdemoros 7B	1 (4%)	8 (32%)	16 (64%)		25	2,60
Valdemoros 1A		8 (47%)	9 (53%)		17	2,53
Valdemoros 7A		3 (27%)	7 (64%)	1 (9%)	11	2,82
Valdemoros 8B	1 (13%)	4 (50%)	3 (38%)		8	2,25
Valdemoros 8C		8 (73%)	3 (27%)		11	2,27
Vargas 8C		11 (23%)	30 (64%)	6 (13%)	47	2,89
Vargas 8B		21 (34%)	39 (63%)	2 (3%)	62	2,69
Casetón 2B		2 (40%)	3 (60%)		5	2,60
Casetón 1A	1 (1%)	25 (32%)	42 (55%)	9 (12%)	77	2,77
Vargas 7	1 (1%)	44 (51%)	32 (37%)	9 (10%)	86	2,57
Valdemoros 3D	1 (2%)	28 (64%)	15 (34%)		44	2,32

Table 17. Mesoloph M2

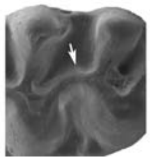
Localities									N
Sansan			1	(13%)	7	(88%)			8
Las Umbrias 20	1	(4%)	12	(43%)	14	(50%)	1	(4%)	28
Las Umbrias 19			5	(42%)	7	(58%)			12
Las Planas 4BA	2	(6%)	11	(31%)	21	(60%)	1	(3%)	35
Las Umbrias 14	1	(5%)	14	(70%)	5	(25%)			20
Las Umbrias 18			2	(25%)	6	(75%)			8
Las Umbrias 17			6	(38%)	9	(56%)	1	(6%)	16
Las Umbrias 12	3	(9%)	22	(65%)	9	(26%)			34
Las Umbrias 16			15	(43%)	20	(57%)			35
Las Umbrias 11	2	(3%)	23	(34%)	42	(63%)			67
Las Umbrias 10			6	(55%)	5	(45%)			11
Las Umbrias 9			4	(40%)	6	(60%)			10
Las Umbrias 8			12	(50%)	12	(50%)			24
Las Umbrias 7	1	(4%)	15	(65%)	7	(30%)			23
Valdemoros 7G	1	(25%)	2	(50%)	1	(25%)			4
Valdemoros 7F			12	(67%)	6	(33%)			18
Valdemoros 7E			13	(68%)	6	(32%)			19
Las Umbrias 5			5	(83%)	1	(17%)			6
Los Umbrias 4	1	(4%)	16	(67%)	7	(29%)			24
Valdemoros 7D	2	(15%)	7	(54%)	4	(31%)			13
Las Umbrias 3	2	(13%)	7	(44%)	7	(44%)			16
Vargas 11	2	(20%)	2	(20%)	6	(60%)			10
Las Umbrias 2			3	(43%)	4	(57%)			7
Las Umbrias 1			7	(58%)	5	(42%)			12
Valdemoros 3F	6	(22%)	18	(67%)	3	(11%)			27
Valdemoros 3E	7	(18%)	26	(65%)	7	(18%)			40
Valdemoros 7C			13	(43%)	17	(57%)			30
Valdemoros 7B	1	(4%)	15	(58%)	10	(38%)			26
Valdemoros 1A	1	(6%)	7	(44%)	8	(50%)			16
Valdemoros 7A			5	(42%)	7	(58%)			12
Valdemoros 8B			3	(38%)	5	(63%)			8
Valdemoros 8C			5	(45%)	6	(55%)			11
Vargas 8C	6	(13%)	35	(73%)	7	(15%)			48
Vargas 8B	2	(3%)	47	(77%)	12	(20%)			61
Casetón 2B			2	(40%)	3	(60%)			5
Casetón 1A	8	(11%)	56	(74%)	11	(14%)	1	(1%)	76
Vargas 7	11	(13%)	46	(54%)	27	(32%)	1	(1%)	85
Valdemoros 3D	11	(26%)	22	(52%)	9	(21%)			42

Table 18. Connection Mesolph-Ectoloph M2

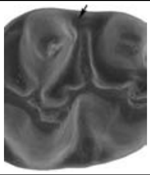
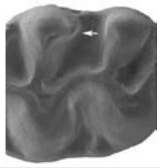
Localities									N
Sansan	4	(50%)	4	(50%)					8
Las Umbrias 20	9	(32%)	14	(50%)	4	(14%)	1	(4%)	28
Las Umbrias 19	3	(23%)	10	(77%)					13
Las Planas 4BA	6	(18%)	27	(79%)			1	(3%)	34
Las Umbrias 14	8	(42%)	11	(58%)					19
Las Umbrias 18	1	(13%)	7	(88%)					8
Las Umbrias 17	3	(19%)	12	(75%)			1	(6%)	16
Las Umbrias 12	17	(50%)	17	(50%)					34
Las Umbrias 16	14	(39%)	22	(61%)					36
Las Umbrias 11	30	(45%)	37	(55%)					67
Las Umbrias 10	5	(45%)	6	(55%)					11
Las Umbrias 9	5	(50%)	5	(50%)					10
Las Umbrias 8	11	(46%)	13	(54%)					24
Las Umbrias 7	13	(59%)	9	(41%)					22
Valdemoros 7G	1	(25%)	3	(75%)					4
Valdemoros 7F	10	(59%)	7	(41%)					17
Valdemoros 7E	7	(37%)	12	(63%)					19
Las Umbrias 5	3	(50%)	3	(50%)					6
Los Umbrias 4	12	(52%)	11	(48%)					23
Valdemoros 7D	4	(31%)	7	(54%)	2	(15%)			13
Las Umbrias 3	4	(27%)	11	(73%)					15
Vargas 11	2	(20%)	8	(80%)					10
Las Umbrias 2	1	(17%)	5	(83%)					6
Las Umbrias 1	3	(25%)	9	(75%)					12
Valdemoros 3F	13	(50%)	12	(46%)	1	(4%)			26
Valdemoros 3E	14	(36%)	24	(62%)	1	(3%)			39
Valdemoros 7C	6	(23%)	19	(73%)	1	(4%)			26
Valdemoros 7B	7	(28%)	17	(68%)	1	(4%)			25
Valdemoros 1A	3	(19%)	13	(81%)					16
Valdemoros 7A	2	(18%)	9	(82%)					11
Valdemoros 8B	1	(13%)	6	(75%)	1	(13%)			8
Valdemoros 8C	5	(45%)	6	(55%)					11
Vargas 8C	21	(45%)	26	(55%)					47
Vargas 8B	26	(43%)	35	(57%)					61
Casetón 2B			5	(100%)					5
Casetón 1A	22	(29%)	51	(68%)	1	(1%)	1	(1%)	75
Vargas 7	18	(21%)	65	(77%)	1	(1%)			84
Valdemoros 3D	14	(33%)	27	(64%)	1	(2%)			42

Table 19. Metalophule M2

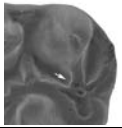
Localities									N
Sansan		5 (100%)							5
Las Umbrias 20		14 (74%)			2 (11%)			3 (16%)	19
Las Umbrias 19		6 (60%)			2 (20%)	1 (10%)		1 (10%)	10
Las Planas 4BA		16 (55%)	2 (7%)	1 (3%)	4 (14%)	5 (17%)		1 (3%)	29
Las Umbrias 14		12 (63%)		2 (11%)		2 (11%)		3 (16%)	19
Las Umbrias 18		4 (57%)		1 (14%)	1 (14%)			1 (14%)	7
Las Umbrias 17		9 (64%)			2 (14%)	1 (7%)		2 (14%)	14
Las Umbrias 12		23 (88%)		1 (4%)	1 (4%)			1 (4%)	26
Las Umbrias 16		24 (73%)		1 (3%)	1 (3%)	1 (3%)	2 (6%)	4 (12%)	33
Las Umbrias 11	2 (3%)	41 (68%)		4 (7%)	5 (8%)		1 (2%)	7 (12%)	60
Las Umbrias 10		8 (80%)			2 (20%)				10
Las Umbrias 9	5 (56%)							4 (44%)	9
Las Umbrias 8		12 (55%)		2 (9%)	6 (27%)	1 (5%)		1 (5%)	22
Las Umbrias 7		14 (67%)		5 (24%)	1 (5%)			1 (5%)	21
Valdemoros 7G		3 (100%)							3
Valdemoros 7F		10 (63%)		2 (13%)	2 (13%)	1 (6%)		1 (6%)	16
Valdemoros 7E		10 (56%)		2 (11%)	2 (11%)			4 (22%)	18
Las Umbrias 5		4 (67%)			1 (17%)	1 (17%)			6
Los Umbrias 4		13 (59%)		1 (5%)	1 (5%)	1 (5%)		6 (27%)	22
Valdemoros 7D		8 (73%)			1 (9%)		1 (9%)	1 (9%)	11
Las Umbrias 3		10 (71%)		1 (7%)	1 (7%)			2 (14%)	14
Vargas 11		7 (88%)					1 (13%)		8
Las Umbrias 2		3 (50%)	2 (33%)					1 (17%)	6
Las Umbrias 1		9 (75%)		1 (8%)				2 (17%)	12
Valdemoros 3F		20 (80%)		2 (8%)	1 (4%)			2 (8%)	25
Valdemoros 3E		29 (76%)		3 (8%)	4 (11%)			2 (5%)	38
Valdemoros 7C	2 (11%)	11 (58%)		1 (5%)	2 (11%)			3 (16%)	19
Valdemoros 7B		14 (61%)		1 (4%)	4 (17%)	2 (9%)		2 (9%)	23
Valdemoros 1A		10 (71%)		1 (7%)	2 (14%)			1 (7%)	14
Valdemoros 7A		5 (63%)			3 (38%)				8
Valdemoros 8B		4 (50%)		1 (13%)	2 (25%)			1 (13%)	8
Valdemoros 8C		4 (57%)			1 (14%)		1 (14%)	1 (14%)	7
Vargas 8C		34 (76%)	3 (7%)	3 (7%)	3 (7%)			2 (4%)	45
Vargas 8B	1 (2%)	45 (83%)		2 (4%)	4 (7%)			2 (4%)	54
Casetón 2B		4 (80%)					1 (20%)		5
Casetón 1A		50 (70%)		6 (8%)	8 (11%)	1 (1%)		6 (8%)	71
Vargas 7		49 (68%)	1 (1%)	6 (8%)	13 (18%)		1 (1%)	2 (3%)	72
Valdemoros 3D		27 (87%)	1 (3%)					3 (10%)	31

Table 20. Anterior Metalophule M2

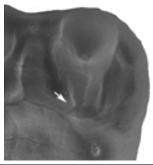
Localities			N
Sansan	5 (100%)		5
Las Umbrias 20	14 (100%)		14
Las Umbrias 19	6 (100%)		6
Las Planas 4BA	18 (100%)		18
Las Umbrias 14	12 (100%)		12
Las Umbrias 18	4 (100%)		4
Las Umbrias 17	9 (100%)		9
Las Umbrias 12	21 (91%)	2 (9%)	23
Las Umbrias 16	23 (96%)	1 (4%)	24
Las Umbrias 11	39 (95%)	2 (5%)	41
Las Umbrias 10	7 (88%)	1 (13%)	8
Las Umbrias 9	5 (100%)		5
Las Umbrias 8	12 (100%)		12
Las Umbrias 7	13 (93%)	1 (7%)	14
Valdemoros 7G	3 (100%)		3
Valdemoros 7F	10 (100%)		10
Valdemoros 7E	8 (80%)	2 (20%)	10
Las Umbrias 5	4 (100%)		4
Los Umbrias 4	13 (100%)		13
Valdemoros 7D	8 (100%)		8
Las Umbrias 3	9 (90%)	1 (10%)	10
Vargas 11	7 (100%)		7
Las Umbrias 2	5 (100%)		5
Las Umbrias 1	9 (100%)		9
Valdemoros 3F	20 (100%)		20
Valdemoros 3E	28 (97%)	1 (3%)	29
Valdemoros 7C	10 (91%)	1 (9%)	11
Valdemoros 7B	13 (93%)	1 (7%)	14
Valdemoros 1A	10 (100%)		10
Valdemoros 7A	5 (100%)		5
Valdemoros 8B	5 (100%)		5
Valdemoros 8C	4 (100%)		4
Vargas 8C	33 (89%)	4 (11%)	37
Vargas 8B	40 (89%)	5 (11%)	45
Casetón 2B	3 (75%)	1 (25%)	4
Casetón 1A	49 (98%)	1 (2%)	50
Vargas 7	48 (96%)	2 (4%)	50
Valdemoros 3D	27 (96%)	1 (4%)	28

Table 21. Metalophule M3

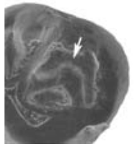
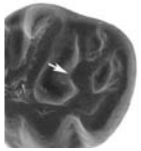
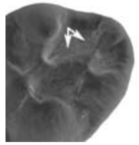
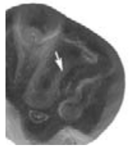
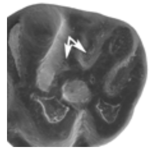
Localities								N
Las Umbrias 20	1 (25%)		1 (75%)					2
Las Umbrias 19	2 (50%)	1 (25%)			1 (25%)			4
Las Umbrias 14		2 (67%)	1 (33%)					3
Las Umbrias 18	1 (100%)							1
Las Umbrias 12			2 (50%)		2 (50%)			4
Las Umbrias 16					1 (100%)			1
Las Umbrias 11	3 (50%)		1 (17%)		2 (33%)			6
Las Umbrias 10		1 (33%)	1 (33%)		1 (33%)			3
Las Umbrias 9			1 (50%)	1 (50%)				2
Las Umbrias 8	1 (50%)				1 (50%)			2
Las Umbrias 7		1 (50%)			1 (50%)			2
Valdemoros 7F			1 (25%)	1 (25%)	2 (50%)			4
Valdemoros 3E		2 (50%)	2 (50%)					4
Valdemoros 1A		1 (17%)	2 (33%)	1 (17%)	2 (33%)			6
Vargas 8C		3 (100%)						3
Casetón 2B		1 (50%)	1 (50%)					2
Casetón 1A	4 (16%)	9 (36%)	8 (32%)	1 (4%)	1 (4%)	1 (4%)	1 (4%)	25
Vargas 7	1 (33%)		2 (67%)					3
Valdemoros 3D		1 (100%)						1

Table 22. Anteroconid m1

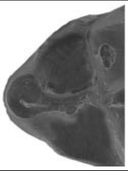
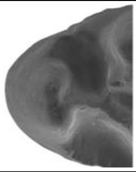
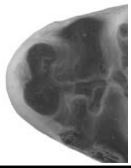
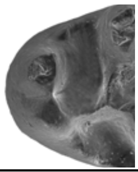
Localities					N	MV
Sansan	4 (21%)	12 (63%)	3 (16%)		19	1,95
Las Umbrias 20	14 (64%)	4 (18%)	4 (18%)		22	1,55
Las Umbrias 19	15 (68%)	3 (14%)	3 (14%)	1 (5%)	22	1,55
Las Planas 4BA	22 (67%)	5 (15%)	6 (18%)		33	1,52
Las Umbrias 14	20 (80%)	4 (16%)	1 (4%)		25	1,24
Las Umbrias 18	5 (83%)	1 (17%)			6	1,17
Las Umbrias 17	9 (53%)	6 (35%)	2 (12%)		17	1,59
Las Umbrias 12	17 (74%)	5 (22%)	1 (4%)		23	1,30
Las Umbrias 16	14 (64%)	6 (27%)	2 (9%)		22	1,45
Las Umbrias 11	37 (57%)	19 (29%)	8 (12%)	1 (2%)	65	1,58
Las Umbrias 10	7 (47%)	6 (40%)	2 (13%)		15	1,67
Las Umbrias 9	13 (57%)	9 (39%)	1 (4%)		23	1,48
Las Umbrias 8	13 (72%)	3 (17%)	2 (11%)		18	1,39
Las Umbrias 7	5 (42%)	3 (25%)	4 (33%)		12	1,92
Valdemoros 7G		1 (50%)	1 (50%)		2	2,50
Valdemoros 7F	13 (100%)				13	1,00
Valdemoros 7E	16 (84%)	3 (16%)			19	1,16
Las Umbrias 5	4 (67%)	1 (17%)	1 (17%)		6	1,50
Los Umbrias 4	14 (82%)	2 (12%)	1 (6%)		17	1,24
Valdemoros 7D	2 (33%)	2 (33%)	2 (33%)		6	2,00
Las Umbrias 3	9 (100%)				9	1,00
Vargas 11	4 (80%)	1 (20%)			5	1,20
Las Umbrias 2	8 (67%)	4 (33%)			12	1,33
Las Umbrias 1	8 (100%)				8	1,00
Valdemoros 3F	20 (100%)				20	1,00
Valdemoros 3E	40 (82%)	7 (14%)	2 (4%)		49	1,22
Valdemoros 7C	23 (96%)		1 (4%)		24	1,08
Valdemoros 7B	16 (94%)	1 (6%)			17	1,06
Valdemoros 1A	26 (96%)	1 (4%)			27	1,04
Valdemoros 7A	12 (86%)	2 (14%)			14	1,14
Valdemoros 8B	3 (100%)				3	1,00
Valdemoros 8C	3 (100%)				3	1,00
Vargas 8C	32 (89%)	4 (11%)			36	1,11
Vargas 8B	37 (86%)	5 (12%)	1 (2%)		43	1,16
Casetón 2B	7 (88%)	1 (13%)			8	1,13
Casetón 1A	43 (81%)	9 (17%)	1 (2%)		53	1,21
Vargas 7	66 (85%)	9 (12%)	3 (4%)		78	1,19
Valdemoros 3D	25 (83%)	5 (17%)			30	1,17

Table 23. Antero-lingual cingulid of the m1

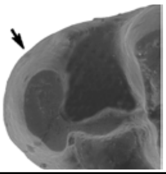
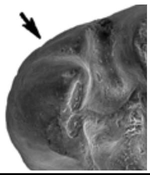
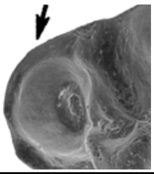
Localities				N
Las Umbrias 12	23 (92%)	1 (4%)	1 (4%)	25
Las Umbrias 16	17 (81%)	2 (10%)	2 (10%)	21
Las Umbrias 11	59 (88%)	3 (4%)	5 (7%)	67
Las Umbrias 10	12 (80%)	1 (7%)	2 (13%)	15
Las Umbrias 9	21 (100%)			21
Las Umbrias 8	21 (100%)			21
Las Umbrias 7	11 (92%)		1 (8%)	12
Las Umbrias 5	5 (83%)		1 (17%)	6
Los Umbrias 4	18 (100%)			18
Valdemoros 7D	6 (100%)			6
Las Umbrias 3	8 (100%)			8
Vargas 11	5 (100%)			5
Las Umbrias 2	9 (82%)	2 (18%)		11
Las Umbrias 1	6 (75%)	1 (13%)	1 (13%)	8
Valdemoros 3F	16 (76%)		5 (24%)	21
Valdemoros 3E	44 (90%)		5 (10%)	49
Valdemoros 7C	21 (91%)	2 (9%)		23
Valdemoros 7B	15 (94%)	1 (6%)		16
Valdemoros 1A	18 (72%)	3 (12%)	4 (16%)	25
Valdemoros 7A	13 (93%)	1 (7%)		14
Valdemoros 8B	2 (100%)			2
Valdemoros 8C	3 (100%)			3
Vargas 8C	30 (79%)	2 (5%)	6 (16%)	38
Vargas 8B	31 (72%)	3 (7%)	9 (21%)	43
Casetón 2B	7 (88%)		1 (13%)	8
Casetón 1A	37 (71%)	2 (4%)	13 (25%)	52
Vargas 7	50 (64%)	2 (3%)	26 (33%)	78
Valdemoros 3D	20 (63%)	2 (6%)	10 (31%)	32

Table 24. Antero-labial cingulid of the m1

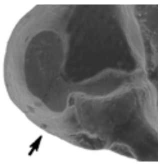
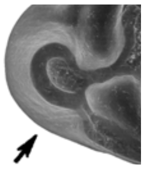
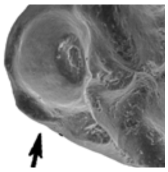
Localities				N
Las Umbrias 12	26 (100%)			26
Las Umbrias 16	23 (100%)			23
Las Umbrias 11	64 (97%)	1 (2%)	1 (2%)	66
Las Umbrias 10	13 (93%)		1 (7%)	14
Las Umbrias 9	24 (100%)			24
Las Umbrias 8	18 (100%)			18
Las Umbrias 7	13 (100%)			13
Las Umbrias 5	4 (67%)		2 (33%)	6
Los Umbrias 4	18 (100%)			18
Valdemoros 7D	6 (100%)			6
Las Umbrias 3	10 (100%)			10
Vargas 11	5 (100%)			5
Las Umbrias 2	13 (100%)			13
Las Umbrias 1	8 (100%)			8
Valdemoros 3F	17 (81%)	2 (10%)	2 (10%)	21
Valdemoros 3E	48 (96%)		2 (4%)	50
Valdemoros 7C	25 (100%)			25
Valdemoros 7B	16 (94%)	1 (6%)		17
Valdemoros 1A	23 (88%)	3 (12%)		26
Valdemoros 7A	11 (79%)	1 (7%)	2 (14%)	14
Valdemoros 8B	3 (100%)			3
Valdemoros 8C	3 (100%)			3
Vargas 8C	35 (97%)	1 (3%)		36
Vargas 8B	41 (95%)		2 (5%)	43
Casetón 2B	8 (100%)			8
Casetón 1A	47 (87%)	3 (6%)	4 (7%)	54
Vargas 7	65 (84%)	5 (6%)	7 (9%)	77
Valdemoros 3D	30 (91%)		3 (9%)	33

Table 25. Labial Spur of the Anterolophulid m1

Localities				N
Sansan	23 (96%)		1 (4%)	24
Las Umbrias 12	28 (93%)	1 (3%)	1 (3%)	30
Las Umbrias 16	30 (100%)			30
Las Umbrias 11	72 (97%)	1 (1%)	1 (1%)	74
Las Umbrias 10	18 (100%)			18
Las Umbrias 9	24 (96%)		1 (4%)	25
Las Umbrias 8	25 (100%)			25
Las Umbrias 7	15 (100%)			15
Valdemoros 7G	2 (100%)			2
Valdemoros 7F	15 (100%)			15
Valdemoros 7E	22 (96%)		1 (4%)	23
Las Umbrias 5	6 (100%)			6
Los Umbrias 4	20 (95%)		1 (5%)	21
Valdemoros 7D	6 (100%)			6
Las Umbrias 3	13 (100%)			13
Vargas 11	5 (63%)	1 (13%)	2 (25%)	8
Las Umbrias 2	13 (87%)		2 (13%)	15
Las Umbrias 1	10 (100%)			10
Valdemoros 3F	19 (90%)	1 (5%)	1 (5%)	21
Valdemoros 3E	53 (98%)		1 (2%)	54
Valdemoros 7C	25 (96%)		1 (4%)	26
Valdemoros 7B	17 (100%)			17
Valdemoros 1A	25 (93%)	2 (7%)		27
Valdemoros 7A	18 (95%)		1 (5%)	19
Valdemoros 8B	3 (100%)			3
Valdemoros 8C	3 (60%)		2 (40%)	5
Vargas 8C	35 (92%)	3 (8%)		38
Vargas 8B	42 (91%)	1 (2%)	3 (7%)	46
Casetón 2B	10 (100%)			10
Casetón 1A	51 (89%)	2 (4%)	4 (7%)	57
Vargas 7	73 (90%)	1 (1%)	7 (9%)	81
Valdemoros 3D	32 (100%)			32

Table 26. Metalophulid m1

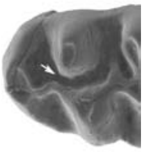
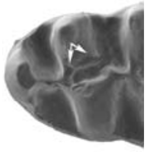
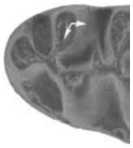
Localities						N
Sansan	1 (3%)	17 (85%)	1 (5%)		1 (5%)	20
Las Umbrias 19		30 (97%)			1 (3%)	31
Las Planas 4BA		32 (89%)	2 (6%)		2 (6%)	36
Las Umbrias 14		23 (85%)	3 (11%)		1 (4%)	27
Las Umbrias 18		7 (70%)	1 (10%)		2 (20%)	10
Las Umbrias 17		18 (100%)				18
Las Umbrias 12		27 (84%)	3 (9%)		2 (6%)	32
Las Umbrias 16		30 (100%)				30
Las Umbrias 11		72 (95%)	1 (1%)		3 (4%)	76
Las Umbrias 10		17 (94%)			1 (6%)	18
Las Umbrias 9		23 (92%)	1 (4%)		1 (4%)	25
Las Umbrias 8		20 (77%)	5 (19%)		1 (4%)	26
Las Umbrias 7		14 (93%)			1 (7%)	15
Valdemoros 7G		2 (100%)				2
Valdemoros 7F		15 (94%)			1 (6%)	16
Valdemoros 7E		20 (91%)			2 (9%)	22
Las Umbrias 5		3 (50%)	1 (17%)		2 (33%)	6
Los Umbrias 4		21 (91%)	2 (9%)			23
Valdemoros 7D		6 (100%)				6
Las Umbrias 3		11 (85%)	1 (8%)		1 (8%)	13
Vargas 11		6 (100%)				6
Las Umbrias 2		13 (93%)	1 (7%)			14
Las Umbrias 1		8 (80%)			2 (20%)	10
Valdemoros 3F	1 (2%)	20 (95%)				21
Valdemoros 3E		47 (96%)	1 (2%)		1 (2%)	49
Valdemoros 7C		29 (100%)				29
Valdemoros 7B		19 (100%)				19
Valdemoros 1A		23 (88%)	3 (12%)			26
Valdemoros 7A		16 (89%)	1 (6%)		1 (6%)	18
Valdemoros 8B		2 (100%)				2
Valdemoros 8C		4 (80%)			1 (20%)	5
Vargas 8C	2 (3%)	38 (95%)				40
Vargas 8B	1 (1%)	42 (91%)	1 (2%)	1 (2%)	1 (2%)	46
Casetón 2B		10 (100%)				10
Casetón 1A	2 (2%)	58 (97%)				60
Vargas 7		72 (100%)				72
Valdemoros 3D		30 (97%)	1 (3%)			31

Table 27. Mesolophid m1

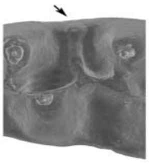
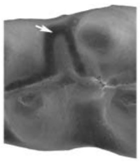
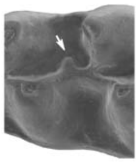
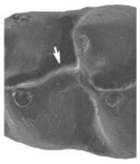
Localities					N	MV
Sansan		2 (9%)	17 (77%)	3 (14%)	22	3,05
Las Umbrias 20		1 (4%)	15 (65%)	7 (30%)	23	3,26
Las Umbrias 19		3 (10%)	18 (58%)	10 (32%)	31	3,23
Las Planas 4BA			31 (76%)	10 (24%)	41	3,24
Las Umbrias 14			21 (72%)	8 (28%)	29	3,28
Las Umbrias 18			7 (70%)	3 (30%)	10	3,30
Las Umbrias 17		1 (5%)	14 (74%)	4 (21%)	19	3,16
Las Umbrias 12			28 (90%)	3 (10%)	31	3,10
Las Umbrias 16		1 (3%)	26 (84%)	4 (13%)	31	3,10
Las Umbrias 11		6 (8%)	66 (85%)	6 (8%)	78	3,00
Las Umbrias 10		2 (11%)	14 (78%)	2 (11%)	18	3,00
Las Umbrias 9			21 (84%)	4 (16%)	25	3,16
Las Umbrias 8			23 (85%)	4 (15%)	27	3,15
Las Umbrias 7		2 (13%)	13 (87%)		15	2,87
Valdemoros 7G			2 (100%)		2	3,00
Valdemoros 7F		1 (6%)	13 (76%)	3 (18%)	17	3,12
Valdemoros 7E		1 (4%)	20 (87%)	2 (9%)	23	3,04
Las Umbrias 5			5 (100%)		5	3,00
Los Umbrias 4		2 (9%)	16 (70%)	5 (22%)	23	3,13
Valdemoros 7D			5 (83%)	1 (17%)	6	3,17
Las Umbrias 3			9 (69%)	4 (31%)	13	3,31
Vargas 11			6 (86%)	1 (14%)	7	3,14
Las Umbrias 2		2 (13%)	13 (87%)		15	2,87
Las Umbrias 1			8 (80%)	2 (20%)	10	3,20
Valdemoros 3F			16 (76%)	5 (24%)	21	3,24
Valdemoros 3E		2 (4%)	43 (86%)	5 (10%)	50	3,06
Valdemoros 7C		1 (4%)	22 (79%)	5 (18%)	28	3,14
Valdemoros 7B			19 (95%)	1 (5%)	20	3,05
Valdemoros 1A			20 (77%)	6 (23%)	26	3,23
Valdemoros 7A		1 (5%)	15 (79%)	3 (16%)	19	3,11
Valdemoros 8B			2 (100%)		2	3,00
Valdemoros 8C			5 (100%)		5	3,00
Vargas 8C	1 (2%)	4 (10%)	34 (81%)	3 (7%)	42	2,93
Vargas 8B		1 (2%)	34 (74%)	11 (24%)	46	3,22
Casetón 2B		2 (20%)	7 (70%)	1 (10%)	10	2,90
Casetón 1A	2 (3%)	4 (7%)	48 (79%)	7 (11%)	61	2,98
Vargas 7		4 (5%)	63 (81%)	11 (14%)	78	3,09
Valdemoros 3D	1 (3%)	2 (5%)	30 (81%)	4 (11%)	37	3,00

Table 28. Ectomesolophid m1

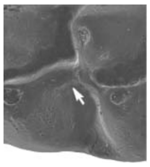
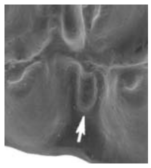
Localities			N
Sansan	24 (100%)		24
Las Umbrias 12	31 (100%)		31
Las Umbrias 16	30 (100%)		30
Las Umbrias 11	78 (100%)		78
Las Umbrias 10	18 (100%)		18
Las Umbrias 9	24 (100%)		24
Las Umbrias 8	27 (100%)		27
Las Umbrias 7	14 (100%)		14
Valdemoros 7G	2 (100%)		2
Valdemoros 7F	18 (100%)		18
Valdemoros 7E	23 (100%)		23
Las Umbrias 5	6 (100%)		6
Los Umbrias 4	21 (100%)		21
Valdemoros 7D	6 (100%)		6
Las Umbrias 3	13 (100%)		13
Vargas 11	6 (100%)		6
Las Umbrias 2	15 (100%)		15
Las Umbrias 1	10 (100%)		10
Valdemoros 3F	20 (100%)		20
Valdemoros 3E	50 (100%)		50
Valdemoros 7C	30 (100%)		30
Valdemoros 7B	20 (100%)		20
Valdemoros 1A	26 (100%)		26
Valdemoros 7A	20 (100%)		20
Valdemoros 8B	4 (100%)		4
Valdemoros 8C	4 (80%)	1 (20%)	5
Vargas 8C	43 (100%)		43
Vargas 8B	48 (100%)		48
Casetón 2B	10 (100%)		10
Casetón 1A	62 (97%)	2 (3%)	64
Vargas 7	84 (99%)	1 (1%)	85
Valdemoros 3D	39 (100%)		39

Table 29. Lingual Anterolophid m2

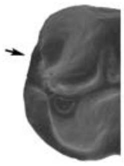
Localities				N	MV
Sansan	2 (9%)	20 (87%)	1 (4%)	23	1,96
Las Umbrias 12	6 (18%)	26 (79%)	1 (3%)	33	1,85
Las Umbrias 16	4 (14%)	24 (86%)		28	1,86
Las Umbrias 11	8 (11%)	58 (83%)	4 (6%)	70	1,94
Las Umbrias 10	2 (25%)	5 (63%)	1 (13%)	8	1,88
Las Umbrias 9	5 (33%)	10 (67%)		15	1,67
Las Umbrias 8	7 (25%)	19 (68%)	2 (7%)	28	1,82
Las Umbrias 7	1 (10%)	8 (80%)	1 (10%)	10	2,00
Valdemoros 7G		3 (100%)		3	2,00
Valdemoros 7F	6 (46%)	6 (46%)	1 (8%)	13	1,62
Valdemoros 7E	7 (30%)	13 (57%)	3 (13%)	23	1,83
Las Umbrias 5	2 (25%)	4 (50%)	2 (25%)	8	2,00
Los Umbrias 4	4 (24%)	13 (76%)		17	1,76
Valdemoros 7D	1 (25%)	3 (75%)		4	1,75
Las Umbrias 3	3 (21%)	9 (64%)	2 (14%)	14	1,93
Vargas 11	1 (14%)	6 (86%)		7	1,86
Las Umbrias 2	1 (11%)	7 (78%)	1 (11%)	9	2,00
Las Umbrias 1	1 (13%)	7 (88%)		8	1,88
Valdemoros 3F	12 (67%)	5 (28%)	1 (6%)	18	1,39
Valdemoros 3E	22 (65%)	12 (35%)		34	1,35
Valdemoros 7C	4 (19%)	16 (76%)	1 (5%)	21	1,86
Valdemoros 7B	6 (18%)	23 (70%)	4 (12%)	33	1,94
Valdemoros 1A	1 (3%)	28 (93%)	1 (3%)	30	2,00
Valdemoros 7A	4 (17%)	19 (83%)		23	1,83
Valdemoros 8B		2 (100%)		2	2,00
Valdemoros 8C	1 (17%)	3 (50%)	2 (33%)	6	2,17
Vargas 8C	19 (50%)	17 (45%)	2 (5%)	38	1,55
Vargas 8B	24 (56%)	18 (42%)	1 (2%)	43	1,47
Casetón 2B		7 (88%)	1 (13%)	8	2,13
Casetón 1A	40 (69%)	16 (28%)	2 (3%)	58	1,34
Vargas 7	47 (59%)	32 (40%)	1 (1%)	80	1,43
Valdemoros 3D	21 (60%)	13 (37%)	1 (3%)	35	1,43

Table 30. Mesolophid m2

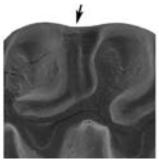
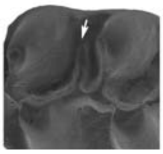
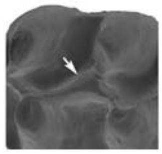
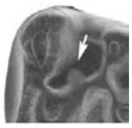
Localities					N	MV
Sansan		8 (27%)	21 (70%)	1 (3%)	30	2,77
Las Umbrias 20		4 (13%)	17 (57%)	9 (30%)	30	3,17
Las Umbrias 19			22 (67%)	11 (33%)	33	3,33
Las Planas 4BA		4 (11%)	22 (63%)	9 (26%)	35	3,14
Las Umbrias 14		1 (3%)	19 (63%)	10 (33%)	30	3,30
Las Umbrias 18			7 (78%)	2 (22%)	9	3,22
Las Umbrias 17		1 (7%)	11 (73%)	3 (20%)	15	3,13
Las Umbrias 12			32 (80%)	8 (20%)	40	3,20
Las Umbrias 16		1 (3%)	25 (69%)	10 (28%)	36	3,25
Las Umbrias 11		3 (4%)	64 (82%)	11 (14%)	78	3,10
Las Umbrias 10			8 (89%)	1 (11%)	9	3,11
Las Umbrias 9		3 (18%)	12 (71%)	2 (12%)	17	2,94
Las Umbrias 8		3 (9%)	25 (71%)	7 (20%)	35	3,11
Las Umbrias 7		3 (25%)	8 (67%)	1 (8%)	12	2,83
Valdemoros 7G			3 (100%)		3	3,00
Valdemoros 7F			14 (93%)	1 (7%)	15	3,07
Valdemoros 7E		3 (10%)	23 (77%)	4 (13%)	30	3,03
Las Umbrias 5		1 (10%)	9 (90%)		10	2,90
Los Umbrias 4	1 (5%)	1 (5%)	16 (84%)	1 (5%)	19	2,89
Valdemoros 7D			5 (100%)		5	3,00
Las Umbrias 3		2 (13%)	10 (63%)	4 (25%)	16	3,13
Vargas 11		1 (14%)	6 (86%)		7	2,86
Las Umbrias 2		2 (17%)	10 (83%)		12	2,83
Las Umbrias 1			8 (89%)	1 (11%)	9	3,11
Valdemoros 3F		1 (5%)	16 (80%)	3 (15%)	20	3,10
Valdemoros 3E		1 (3%)	32 (82%)	6 (15%)	39	3,13
Valdemoros 7C	1 (4%)	5 (19%)	14 (52%)	7 (26%)	27	3,00
Valdemoros 7B		4 (12%)	24 (73%)	5 (15%)	33	3,03
Valdemoros 1A		1 (3%)	24 (77%)	6 (19%)	31	3,16
Valdemoros 7A		3 (12%)	21 (81%)	2 (8%)	26	2,96
Valdemoros 8B				3 (100%)	3	4,00
Valdemoros 8C			2 (29%)	5 (71%)	7	3,71
Vargas 8C			27 (68%)	13 (33%)	40	3,33
Vargas 8B		4 (9%)	27 (60%)	14 (31%)	45	3,22
Casetón 2B			5 (56%)	4 (44%)	9	3,44
Casetón 1A		3 (4%)	48 (68%)	20 (28%)	71	3,24
Vargas 7		1 (1%)	68 (78%)	18 (21%)	87	3,20
Valdemoros 3D			34 (77%)	10 (23%)	44	3,23

Table 31. Lingual Anterolophid m3

Localities				N	MV
Sansan		2 (100%)		2	2,00
Las Umbrias 20		1 (100%)		1	2,00
Las Umbrias 19	2 (20%)	8 (80%)		10	1,80
Las Umbrias 12	1 (13%)	6 (75%)	1 (13%)	8	2,00
Las Umbrias 16	1 (33%)	2 (67%)		3	1,67
Las Umbrias 11		8 (100%)		8	2,00
Las Umbrias 10		2 (100%)		2	2,00
Las Umbrias 9		1 (50%)	1 (50%)	2	2,50
Las Umbrias 8	4 (36%)	7 (64%)		11	1,64
Las Umbrias 7		1 (100%)		1	2,00
Valdemoros 7G			1 (100%)	1	3,00
Valdemoros 7F	1 (50%)	1 (50%)		2	1,50
Los Umbrias 4	3 (100%)			3	1,00
Las Umbrias 3		5 (100%)		5	2,00
Las Umbrias 2	1 (33%)	1 (33%)	1 (33%)	3	2,00
Las Umbrias 1	1 (100%)			1	1,00
Valdemoros 3F		2 (100%)		2	2,00
Valdemoros 3E	1 (20%)	3 (60%)	1 (20%)	5	2,00
Valdemoros 7C		1 (100%)		1	2,00
Valdemoros 1A	2 (33%)	4 (67%)		6	1,67
Vargas 8C	4 (57%)	2 (29%)	1 (14%)	7	1,57
Vargas 8B	2 (33%)	4 (67%)		6	1,67
Casetón 2B		3 (60%)	2 (40%)	5	2,40
Casetón 1A	33 (73%)	7 (16%)	5 (11%)	45	1,38
Vargas 7	2 (29%)	5 (71%)		7	1,71
Valdemoros 3D	3 (75%)		1 (25%)	4	1,50

Table 32. Mesolophid m3

Localities				N
Sansan			2 (100%)	2
Las Umbrias 20			2 (100%)	2
Las Umbrias 19	1 (7%)	1 (7%)	12 (86%)	14
Las Umbrias 14	1 (100%)			1
Las Umbrias 18	2 (100%)			2
Las Umbrias 12			8 (100%)	8
Las Umbrias 16			3 (100%)	3
Las Umbrias 11	2 (25%)		6 (75%)	8
Las Umbrias 10			1 (100%)	1
Las Umbrias 9			2 (100%)	2
Las Umbrias 8			11 (100%)	11
Las Umbrias 7			4 (100%)	4
Valdemoros 7G	1 (100%)			1
Valdemoros 7F			2 (100%)	2
Los Umbrias 4	1 (25%)		3 (75%)	4
Las Umbrias 3			5 (100%)	5
Las Umbrias 2	3 (60%)		2 (40%)	5
Las Umbrias 1			1 (100%)	1
Valdemoros 3F			2 (100%)	2
Valdemoros 3E			5 (100%)	5
Valdemoros 7C	1 (100%)			1
Valdemoros 1A			11 (100%)	11
Vargas 8C	2 (25%)		6 (75%)	8
Vargas 8B	1 (17%)		5 (83%)	6
Casetón 2B			5 (100%)	5
Casetón 1A	1 (2%)		49 (98%)	50
Vargas 7			8 (100%)	8
Valdemoros 3D	1 (14%)		6 (86%)	7

APPENDIX 6.2

Analysis of variance (One-Way ANOVA) for the assemblages of *Megacricetodon collongensis* from the Calatayud-Montalbán Basin.

All analyses were accomplished using exclusively localities with sample sizes larger than five specimens. The localities of Casetones 1A, Casetones 2B and Valdemoros 3E have been omit to maintain data consistency owing to there were data from the bibliography.

Values in red are those where the difference between the means are significant at 0.5.

Table 1. Levene's test of the lower and upper molars of *Megacricetodon collongensis.*

		Levene's test	gl1	gl2	Significance
m1	Length	2,11	8	152	0,038
	Width	0,493	9	212	0,879
m2	Length	0,696	10	206	0,728
	Width	0,685	9	227	0,722
M1	Length	1,006	9	187	0,437
	Width	1,492	9	261	0,151
M2	Length	0,456	11	238	0,928
	Width	0,778	11	248	0,662

Table 2. In the cases that there is homogeneity of variance, we carried out One-Way ANOVA.

		F	Significance
m1	Width	6,549	0,000
m2	Length	5,256	0,000
	Width	4,389	0,000
M1	Length	0,59	0,804
	Width	1,453	0,166
M2	Length	2,405	0,008
	Width	5,577	0,000

Table 3. In the case of the length of the lower first molar, that there is not homogeneity of variance, we carried out Welch and Brown-Forsythe.

			Estadistic	gl1	gl2	Significance
m1	Length	Welch	1,571	8	43,604	0,162
		Brown-Forsythe	1,188	8	44,103	0,328

Table 4. Post hoc of the lower first molars of *Megacricetodon collongensis*. For the length t, we carried out Games-Howell because of the different variances assumed; and for the width we carried out Hochberg's GT2.

		Localities	Localities	Mean Difference	Standard error	Significance
LENGHT m1	Games-Howell	VA1A	VA3D	-0,0035	0,0159	1,0000
			VA3F	-0,0163	0,0242	0,9985
			VA7A	-0,0196	0,0379	0,9996
			VA7B	-0,0181	0,0167	0,9707
			VA7C	-0,0363	0,0158	0,3775
			VR7	-0,0021	0,0138	1,0000
			VR8B	0,0071	0,0146	0,9999
			VR8C	-0,0289	0,0161	0,6828
		VA3D	VA1A	0,0035	0,0159	1,0000
			VA3F	-0,0129	0,0244	0,9997
			VA7A	-0,0162	0,0380	0,9999
			VA7B	-0,0147	0,0169	0,9927
			VA7C	-0,0329	0,0161	0,5325
			VR7	0,0014	0,0142	1,0000
			VR8B	0,0106	0,0149	0,9982
			VR8C	-0,0255	0,0164	0,8195
		VA3F	VA1A	0,0163	0,0242	0,9985
			VA3D	0,0129	0,0244	0,9997
			VA7A	-0,0033	0,0421	1,0000
			VA7B	-0,0018	0,0249	1,0000
			VA7C	-0,0200	0,0243	0,9943
			VR7	0,0142	0,0231	0,9992
			VR8B	0,0235	0,0235	0,9804
			VR8C	-0,0126	0,0245	0,9998
		VA7A	VA1A	0,0196	0,0379	0,9996
			VA3D	0,0162	0,0380	0,9999
			VA3F	0,0033	0,0421	1,0000
			VA7B	0,0015	0,0383	1,0000
			VA7C	-0,0167	0,0379	0,9999
			VR7	0,0176	0,0372	0,9998
			VR8B	0,0268	0,0374	0,9959
			VR8C	-0,0093	0,0381	1,0000
		VA7B	VA1A	0,0181	0,0167	0,9707
			VA3D	0,0147	0,0169	0,9927
			VA3F	0,0018	0,0249	1,0000
			VA7A	-0,0015	0,0383	1,0000
			VA7C	-0,0182	0,0169	0,9716
			VR7	0,0161	0,0150	0,9722
			VR8B	0,0253	0,0157	0,7886
			VR8C	-0,0108	0,0171	0,9992
		VA7C	VA1A	0,0363	0,0158	0,3775
			VA3D	0,0329	0,0161	0,5325
			VA3F	0,0200	0,0243	0,9943
			VA7A	0,0167	0,0379	0,9999
			VA7B	0,0182	0,0169	0,9716
			VR7	0,0342	0,0141	0,3047
			VR8B	0,0435	0,0148	0,1188
			VR8C	0,0074	0,0163	0,9999
		VR7	VA1A	0,0021	0,0138	1,0000
			VA3D	-0,0014	0,0142	1,0000
			VA3F	-0,0142	0,0231	0,9992
			VA7A	-0,0176	0,0372	0,9998
			VA7B	-0,0161	0,0150	0,9722
			VA7C	-0,0342	0,0141	0,3047
			VR8B	0,0092	0,0126	0,9981
			VR8C	-0,0269	0,0144	0,6354
		VR8B	VA1A	-0,0071	0,0146	0,9999
			VA3D	-0,0106	0,0149	0,9982
			VA3F	-0,0235	0,0235	0,9804
			VA7A	-0,0268	0,0374	0,9959
			VA7B	-0,0253	0,0157	0,7886
			VA7C	-0,0435	0,0148	0,1188
			VR7	-0,0092	0,0126	0,9981
			VR8C	-0,0361	0,0151	0,3144
		VR8C	VA1A	0,0289	0,0161	0,6828
			VA3D	0,0255	0,0164	0,8195
			VA3F	0,0126	0,0245	0,9998
			VA7A	0,0093	0,0381	1,0000
			VA7B	0,0108	0,0171	0,9992
			VA7C	-0,0074	0,0163	0,9999
			VR7	0,0269	0,0144	0,6354
			VR8B	0,0361	0,0151	0,3144

		Localities	Localities	Mean Difference	Standard error	Significance
WIDTH m1	Hochberg	LUM1	VA1A	0,0080	0,0158	1,0000
			VA3D	0,0317	0,0159	0,8753
			VA3F	0,0295	0,0165	0,9618
			VA7A	0,0037	0,0174	1,0000
			VA7B	-0,0075	0,0169	1,0000
			VA7C	-0,0229	0,0154	0,9981
			VR7	0,0288	0,0145	0,8772
			VR8B	0,0261	0,0149	0,9734
			VR8C	0,0186	0,0151	1,0000
		VA1A	LUM1	-0,0080	0,0158	1,0000
			VA3D	0,0237	0,0111	0,7721
			VA3F	0,0215	0,0119	0,9561
			VA7A	-0,0043	0,0132	1,0000
			VA7B	-0,0155	0,0124	1,0000
			VA7C	-0,0309	0,0104	0,1319
			VR7	0,0208	0,0090	0,5999
			VR8B	0,0181	0,0097	0,9350
			VR8C	0,0106	0,0100	1,0000
		VA3D	LUM1	-0,0317	0,0159	0,8753
			VA1A	-0,0237	0,0111	0,7721
			VA3F	-0,0021	0,0120	1,0000
			VA7A	-0,0280	0,0133	0,7962
			VA7B	-0,0392	0,0126	0,0888
			VA7C	-0,0546	0,0105	0,0000
			VR7	-0,0029	0,0091	1,0000
			VR8B	-0,0056	0,0098	1,0000
			VR8C	-0,0131	0,0101	0,9999
		VA3F	LUM1	-0,0295	0,0165	0,9618
			VA1A	-0,0215	0,0119	0,9561
			VA3D	0,0021	0,0120	1,0000
			VA7A	-0,0259	0,0140	0,9433
			VA7B	-0,0370	0,0133	0,2242
			VA7C	-0,0524	0,0113	0,0003
			VR7	-0,0007	0,0101	1,0000
			VR8B	-0,0034	0,0107	1,0000
			VR8C	-0,0110	0,0110	1,0000
		VA7A	LUM1	-0,0037	0,0174	1,0000
			VA1A	0,0043	0,0132	1,0000
			VA3D	0,0280	0,0133	0,7962
			VA3F	0,0259	0,0140	0,9433
			VA7B	-0,0112	0,0144	1,0000
			VA7C	-0,0266	0,0127	0,8046
			VR7	0,0251	0,0116	0,7413
			VR8B	0,0224	0,0121	0,9449
			VR8C	0,0149	0,0124	1,0000

Width m1 continued

		Localities	Localities	Mean Difference	Standard error	Significance
WIDTH m1	Hochberg	VA7B	LUM1	0,0075	0,0169	1,0000
			VA1A	0,0155	0,0124	1,0000
			VA3D	0,0392	0,0126	0,0888
			VA3F	0,0370	0,0133	0,2242
			VA7A	0,0112	0,0144	1,0000
			VA7C	-0,0154	0,0119	0,9999
			VR7	0,0363	0,0107	0,0373
			VR8B	0,0336	0,0113	0,1391
			VR8C	0,0261	0,0116	0,6697
		VA7C	LUM1	0,0229	0,0154	0,9981
			VA1A	0,0309	0,0104	0,1319
			VA3D	0,0546	0,0105	0,0000
			VA3F	0,0524	0,0113	0,0003
			VA7A	0,0266	0,0127	0,8046
			VA7B	0,0154	0,0119	0,9999
			VR7	0,0517	0,0082	0,0000
			VR8B	0,0490	0,0090	0,0000
			VR8C	0,0415	0,0093	0,0006
		VR7	LUM1	-0,0288	0,0145	0,8772
			VA1A	-0,0208	0,0090	0,5999
			VA3D	0,0029	0,0091	1,0000
			VA3F	0,0007	0,0101	1,0000
			VA7A	-0,0251	0,0116	0,7413
			VA7B	-0,0363	0,0107	0,0373
			VA7C	-0,0517	0,0082	0,0000
			VR8B	-0,0027	0,0073	1,0000
			VR8C	-0,0102	0,0077	0,9998
		VR8B	LUM1	-0,0261	0,0149	0,9734
			VA1A	-0,0181	0,0097	0,9350
			VA3D	0,0056	0,0098	1,0000
			VA3F	0,0034	0,0107	1,0000
			VA7A	-0,0224	0,0121	0,9449
			VA7B	-0,0336	0,0113	0,1391
			VA7C	-0,0490	0,0090	0,0000
			VR7	0,0027	0,0073	1,0000
			VR8C	-0,0075	0,0085	1,0000
		VR8C	LUM1	-0,0186	0,0151	1,0000
			VA1A	-0,0106	0,0100	1,0000
			VA3D	0,0131	0,0101	0,9999
			VA3F	0,0110	0,0110	1,0000
			VA7A	-0,0149	0,0124	1,0000
			VA7B	-0,0261	0,0116	0,6697
			VA7C	-0,0415	0,0093	0,0006
			VR7	0,0102	0,0077	0,9998
			VR8B	0,0075	0,0085	1,0000

Table 5. Post hoc of the lower second molars of *Megacricetodon collongensis* Both for the length and width of the m2, we carried out Hochberg's GT2 due to the equal variances assumed.

		Localities	Localities	Mean Difference	Standard error	Significance
LENGTH m2	Hochberg	LUM1	VA1A	-0,0286	0,0190	0,9993
			VA3D	0,0117	0,0184	1,0000
			VA3F	0,0008	0,0200	1,0000
			VA7A	-0,0400	0,0193	0,8777
			VA7B	-0,0207	0,0184	1,0000
			VA7C	-0,0244	0,0188	1,0000
			VA8C	-0,0013	0,0243	1,0000
			VR7	0,0182	0,0174	1,0000
			VR8B	0,0085	0,0180	1,0000
			VR8C	-0,0220	0,0184	1,0000
		VA1A	LUM1	0,0286	0,0190	0,9993
			VA3D	0,0403	0,0129	0,1076
			VA3F	0,0295	0,0151	0,9367
			VA7A	-0,0114	0,0142	1,0000
			VA7B	0,0079	0,0128	1,0000
			VA7C	0,0042	0,0134	1,0000
			VA8C	0,0273	0,0204	1,0000
			VR7	0,0468	0,0113	0,0029
			VR8B	0,0371	0,0123	0,1465
			VR8C	0,0066	0,0128	1,0000
		VA3D	LUM1	-0,0117	0,0184	1,0000
			VA1A	-0,0403	0,0129	0,1076
			VA3F	-0,0108	0,0144	1,0000
			VA7A	-0,0517	0,0134	0,0085
			VA7B	-0,0324	0,0119	0,3218
			VA7C	-0,0361	0,0125	0,2141
			VA8C	-0,0130	0,0198	1,0000
			VR7	0,0065	0,0103	1,0000
			VR8B	-0,0032	0,0114	1,0000
			VR8C	-0,0337	0,0119	0,2460
		VA3F	LUM1	-0,0008	0,0200	1,0000
			VA1A	-0,0295	0,0151	0,9367
			VA3D	0,0108	0,0144	1,0000
			VA7A	-0,0408	0,0155	0,3854
			VA7B	-0,0216	0,0143	0,9992
			VA7C	-0,0252	0,0148	0,9913
			VA8C	-0,0022	0,0213	1,0000
			VR7	0,0173	0,0130	1,0000
			VR8B	0,0076	0,0138	1,0000
			VR8C	-0,0229	0,0143	0,9973
		VA7A	LUM1	0,0400	0,0193	0,8777
			VA1A	0,0114	0,0142	1,0000
			VA3D	0,0517	0,0134	0,0085
			VA3F	0,0408	0,0155	0,3854
			VA7B	0,0193	0,0133	0,9997
			VA7C	0,0156	0,0138	1,0000
			VA8C	0,0387	0,0207	0,9639
			VR7	0,0582	0,0119	0,0001
			VR8B	0,0485	0,0128	0,0112
			VR8C	0,0180	0,0133	0,9999

Length m2 continued

		Localities	Localities	Mean Difference	Standard error	Significance
LENGTH m2	Hochberg	VA7B	LUM1	0,0207	0,0184	1,0000
			VA1A	-0,0079	0,0128	1,0000
			VA3D	0,0324	0,0119	0,3218
			VA3F	0,0216	0,0143	0,9992
			VA7A	-0,0193	0,0133	0,9997
			VA7C	-0,0037	0,0124	1,0000
			VA8C	0,0194	0,0198	1,0000
			VR7	0,0389	0,0102	0,0098
			VR8B	0,0292	0,0113	0,4231
			VR8C	-0,0013	0,0118	1,0000
		VA7C	LUM1	0,0244	0,0188	1,0000
			VA1A	-0,0042	0,0134	1,0000
			VA3D	0,0361	0,0125	0,2141
			VA3F	0,0252	0,0148	0,9913
			VA7A	-0,0156	0,0138	1,0000
			VA7B	0,0037	0,0124	1,0000
			VA8C	0,0231	0,0201	1,0000
			VR7	0,0425	0,0109	0,0069
			VR8B	0,0328	0,0119	0,2878
			VR8C	0,0024	0,0124	1,0000
		VA8C	LUM1	0,0013	0,0243	1,0000
			VA1A	-0,0273	0,0204	1,0000
			VA3D	0,0130	0,0198	1,0000
			VA3F	0,0022	0,0213	1,0000
			VA7A	-0,0387	0,0207	0,9639
			VA7B	-0,0194	0,0198	1,0000
			VA7C	-0,0231	0,0201	1,0000
			VR7	0,0195	0,0188	1,0000
			VR8B	0,0098	0,0194	1,0000
			VR8C	-0,0207	0,0198	1,0000
		VR7	LUM1	-0,0182	0,0174	1,0000
			VA1A	-0,0468	0,0113	0,0029
			VA3D	-0,0065	0,0103	1,0000
			VA3F	-0,0173	0,0130	1,0000
			VA7A	-0,0582	0,0119	0,0001
			VA7B	-0,0389	0,0102	0,0098
			VA7C	-0,0425	0,0109	0,0069
			VA8C	-0,0195	0,0188	1,0000
			VR8B	-0,0097	0,0096	1,0000
			VR8C	-0,0402	0,0102	0,0060
		VR8B	LUM1	-0,0085	0,0180	1,0000
			VA1A	-0,0371	0,0123	0,1465
			VA3D	0,0032	0,0114	1,0000
			VA3F	-0,0076	0,0138	1,0000
			VA7A	-0,0485	0,0128	0,0112
			VA7B	-0,0292	0,0113	0,4231
			VA7C	-0,0328	0,0119	0,2878
			VA8C	-0,0098	0,0194	1,0000
			VR7	0,0097	0,0096	1,0000
			VR8C	-0,0305	0,0113	0,3276
		VR8C	LUM1	0,0220	0,0184	1,0000
			VA1A	-0,0066	0,0128	1,0000
			VA3D	0,0337	0,0119	0,2460
			VA3F	0,0229	0,0143	0,9973
			VA7A	-0,0180	0,0133	0,9999
			VA7B	0,0013	0,0118	1,0000
			VA7C	-0,0024	0,0124	1,0000
			VA8C	0,0207	0,0198	1,0000
			VR7	0,0402	0,0102	0,0060
			VR8B	0,0305	0,0113	0,3276

WIDTH m2

Hochberg

Localities	Localities	Mean Difference	Standard error	Significance
LUM1	VA1A	-0,0424	0,0164	0,3648
	VA3D	-0,0101	0,0159	1,0000
	VA3F	-0,0076	0,0167	1,0000
	VA7A	-0,0188	0,0167	1,0000
	VA7B	-0,0329	0,0157	0,8059
	VA7C	-0,0405	0,0163	0,4493
	VR7	0,0010	0,0147	1,0000
	VR8B	-0,0233	0,0155	0,9977
	VR8C	-0,0219	0,0157	0,9995
VA1A	LUM1	0,0424	0,0164	0,3648
	VA3D	0,0323	0,0116	0,2222
	VA3F	0,0348	0,0126	0,2458
	VA7A	0,0235	0,0126	0,9395
	VA7B	0,0095	0,0114	1,0000
	VA7C	0,0019	0,0121	1,0000
	VR7	0,0434	0,0099	0,0008
	VR8B	0,0191	0,0110	0,9771
	VR8C	0,0205	0,0113	0,9547
VA3D	LUM1	0,0101	0,0159	1,0000
	VA1A	-0,0323	0,0116	0,2222
	VA3F	0,0025	0,0120	1,0000
	VA7A	-0,0088	0,0120	1,0000
	VA7B	-0,0229	0,0106	0,7594
	VA7C	-0,0304	0,0114	0,3050
	VR7	0,0111	0,0091	1,0000
	VR8B	-0,0132	0,0103	0,9999
	VR8C	-0,0118	0,0105	1,0000
VA3F	LUM1	0,0076	0,0167	1,0000
	VA1A	-0,0348	0,0126	0,2458
	VA3D	-0,0025	0,0120	1,0000
	VA7A	-0,0113	0,0130	1,0000
	VA7B	-0,0253	0,0118	0,7592
	VA7C	-0,0329	0,0125	0,3286
	VR7	0,0086	0,0104	1,0000
	VR8B	-0,0157	0,0115	0,9996
	VR8C	-0,0143	0,0117	1,0000
VA7A	LUM1	0,0188	0,0167	1,0000
	VA1A	-0,0235	0,0126	0,9395
	VA3D	0,0088	0,0120	1,0000
	VA3F	0,0113	0,0130	1,0000
	VA7B	-0,0141	0,0118	1,0000
	VA7C	-0,0216	0,0125	0,9765
	VR7	0,0198	0,0104	0,9190
	VR8B	-0,0045	0,0115	1,0000
	VR8C	-0,0030	0,0117	1,0000
VA7B	LUM1	0,0329	0,0157	0,8059
	VA1A	-0,0095	0,0114	1,0000
	VA3D	0,0229	0,0106	0,7594
	VA3F	0,0253	0,0118	0,7592
	VA7A	0,0141	0,0118	1,0000
	VA7C	-0,0075	0,0112	1,0000
	VR7	0,0339	0,0088	0,0067
	VR8B	0,0096	0,0100	1,0000
	VR8C	0,0110	0,0103	1,0000
VA7C	LUM1	0,0405	0,0163	0,4493
	VA1A	-0,0019	0,0121	1,0000
	VA3D	0,0304	0,0114	0,3050
	VA3F	0,0329	0,0125	0,3286
	VA7A	0,0216	0,0125	0,9765
	VA7B	0,0075	0,0112	1,0000
	VR7	0,0415	0,0097	0,0013
	VR8B	0,0172	0,0109	0,9944
	VR8C	0,0186	0,0111	0,9857
VR7	LUM1	-0,0010	0,0147	1,0000
	VA1A	-0,0434	0,0099	0,0008
	VA3D	-0,0111	0,0091	1,0000
	VA3F	-0,0086	0,0104	1,0000
	VA7A	-0,0198	0,0104	0,9190
	VA7B	-0,0339	0,0088	0,0067
	VA7C	-0,0415	0,0097	0,0013
	VR8B	-0,0243	0,0084	0,1634
	VR8C	-0,0229	0,0087	0,3268
VR8B	LUM1	0,0233	0,0155	0,9977
	VA1A	-0,0191	0,0110	0,9771
	VA3D	0,0132	0,0103	0,9999
	VA3F	0,0157	0,0115	0,9996
	VA7A	0,0045	0,0115	1,0000
	VA7B	-0,0096	0,0100	1,0000
	VA7C	-0,0172	0,0109	0,9944
	VR7	0,0243	0,0084	0,1634
	VR8C	0,0014	0,0099	1,0000
VR8C	LUM1	0,0219	0,0157	0,9995
	VA1A	-0,0205	0,0113	0,9547
	VA3D	0,0118	0,0105	1,0000
	VA3F	0,0143	0,0117	1,0000
	VA7A	0,0030	0,0117	1,0000
	VA7B	-0,0110	0,0103	1,0000
	VA7C	-0,0186	0,0111	0,9857
	VR7	0,0229	0,0087	0,3268
	VR8B	-0,0014	0,0099	1,0000

Table 6. Post hoc of the upper first molars of *Megacricetodon collongensis*. Both for the length t and width of the M1, we carried out Hochberg's GT2 due to the equal variances assumed.

		Localities	Localities	Mean Difference	Standard error	Significance
LENGTH M1	Hochberg	LUM1	VA1A	0,0079	0,0297	1,0000
			VA3D	0,0280	0,0320	1,0000
			VA3F	-0,0072	0,0308	1,0000
			VA7A	0,0220	0,0302	1,0000
			VA7B	-0,0007	0,0302	1,0000
			VA7C	0,0120	0,0286	1,0000
			VR7	0,0149	0,0277	1,0000
			VR8B	0,0185	0,0282	1,0000
			VR8C	-0,0016	0,0286	1,0000
		VA1A	LUM1	-0,0079	0,0297	1,0000
			VA3D	0,0201	0,0233	1,0000
			VA3F	-0,0151	0,0215	1,0000
			VA7A	0,0141	0,0207	1,0000
			VA7B	-0,0085	0,0207	1,0000
			VA7C	0,0041	0,0184	1,0000
			VR7	0,0070	0,0169	1,0000
			VR8B	0,0106	0,0176	1,0000
			VR8C	-0,0095	0,0184	1,0000
		VA3D	LUM1	-0,0280	0,0320	1,0000
			VA1A	-0,0201	0,0233	1,0000
			VA3F	-0,0352	0,0246	0,9990
			VA7A	-0,0060	0,0239	1,0000
			VA7B	-0,0287	0,0239	1,0000
			VA7C	-0,0160	0,0219	1,0000
			VR7	-0,0131	0,0206	1,0000
			VR8B	-0,0095	0,0213	1,0000
			VR8C	-0,0296	0,0219	0,9997
		VA3F	LUM1	0,0072	0,0308	1,0000
			VA1A	0,0151	0,0215	1,0000
			VA3D	0,0352	0,0246	0,9990
			VA7A	0,0292	0,0221	0,9998
			VA7B	0,0066	0,0221	1,0000
			VA7C	0,0192	0,0200	1,0000
			VR7	0,0222	0,0186	1,0000
			VR8B	0,0257	0,0193	0,9998
			VR8C	0,0056	0,0200	1,0000
		VA7A	LUM1	-0,0220	0,0302	1,0000
			VA1A	-0,0141	0,0207	1,0000
			VA3D	0,0060	0,0239	1,0000
			VA3F	-0,0292	0,0221	0,9998
			VA7B	-0,0227	0,0213	1,0000
			VA7C	-0,0100	0,0191	1,0000
			VR7	-0,0071	0,0176	1,0000
			VR8B	-0,0035	0,0184	1,0000
			VR8C	-0,0236	0,0191	1,0000

Length M1 continued

		Localities	Localities	Mean Difference	Standard error	Significance
LENGTH M1	Hochberg	VA7B	LUM1	0,0007	0,0302	1,0000
			VA1A	0,0085	0,0207	1,0000
			VA3D	0,0287	0,0239	1,0000
			VA3F	-0,0066	0,0221	1,0000
			VA7A	0,0227	0,0213	1,0000
			VA7C	0,0127	0,0191	1,0000
			VR7	0,0156	0,0176	1,0000
			VR8B	0,0191	0,0184	1,0000
			VR8C	-0,0009	0,0191	1,0000
		VA7C	LUM1	-0,0120	0,0286	1,0000
			VA1A	-0,0041	0,0184	1,0000
			VA3D	0,0160	0,0219	1,0000
			VA3F	-0,0192	0,0200	1,0000
			VA7A	0,0100	0,0191	1,0000
			VA7B	-0,0127	0,0191	1,0000
			VR7	0,0029	0,0148	1,0000
			VR8B	0,0065	0,0157	1,0000
			VR8C	-0,0136	0,0165	1,0000
		VR7	LUM1	-0,0149	0,0277	1,0000
			VA1A	-0,0070	0,0169	1,0000
			VA3D	0,0131	0,0206	1,0000
			VA3F	-0,0222	0,0186	1,0000
			VA7A	0,0071	0,0176	1,0000
			VA7B	-0,0156	0,0176	1,0000
			VA7C	-0,0029	0,0148	1,0000
			VR8B	0,0035	0,0139	1,0000
			VR8C	-0,0165	0,0148	1,0000
		VR8B	LUM1	-0,0185	0,0282	1,0000
			VA1A	-0,0106	0,0176	1,0000
			VA3D	0,0095	0,0213	1,0000
			VA3F	-0,0257	0,0193	0,9998
			VA7A	0,0035	0,0184	1,0000
			VA7B	-0,0191	0,0184	1,0000
			VA7C	-0,0065	0,0157	1,0000
			VR7	-0,0035	0,0139	1,0000
			VR8C	-0,0201	0,0157	0,9999
		VR8C	LUM1	0,0016	0,0286	1,0000
			VA1A	0,0095	0,0184	1,0000
			VA3D	0,0296	0,0219	0,9997
			VA3F	-0,0056	0,0200	1,0000
			VA7A	0,0236	0,0191	1,0000
			VA7B	0,0009	0,0191	1,0000
			VA7C	0,0136	0,0165	1,0000
			VR7	0,0165	0,0148	1,0000
			VR8B	0,0201	0,0157	0,9999

		Localities	Localities	Mean Difference	Standard error	Significance
WITDTH M1	Hochberg	LUM1	VA1A	0,0229	0,0190	1,0000
			VA3D	0,0265	0,0190	0,9995
			VA3F	0,0317	0,0192	0,9883
			VA7A	0,0217	0,0192	1,0000
			VA7B	0,0162	0,0192	1,0000
			VA7C	0,0173	0,0181	1,0000
			VR7	0,0390	0,0172	0,6512
			VR8B	0,0356	0,0174	0,8434
			VR8C	0,0220	0,0179	1,0000
		VA1A	LUM1	-0,0229	0,0190	1,0000
			VA3D	0,0037	0,0140	1,0000
			VA3F	0,0089	0,0142	1,0000
			VA7A	-0,0011	0,0142	1,0000
			VA7B	-0,0067	0,0142	1,0000
			VA7C	-0,0055	0,0127	1,0000
			VR7	0,0161	0,0113	0,9992
			VR8B	0,0128	0,0117	1,0000
			VR8C	-0,0009	0,0123	1,0000
		VA3D	LUM1	-0,0265	0,0190	0,9995
			VA1A	-0,0037	0,0140	1,0000
			VA3F	0,0052	0,0142	1,0000
			VA7A	-0,0048	0,0142	1,0000
			VA7B	-0,0104	0,0142	1,0000
			VA7C	-0,0092	0,0127	1,0000
			VR7	0,0124	0,0113	1,0000
			VR8B	0,0091	0,0117	1,0000
			VR8C	-0,0046	0,0123	1,0000
		VA3F	LUM1	-0,0317	0,0192	0,9883
			VA1A	-0,0089	0,0142	1,0000
			VA3D	-0,0052	0,0142	1,0000
			VA7A	-0,0100	0,0144	1,0000
			VA7B	-0,0156	0,0144	1,0000
			VA7C	-0,0144	0,0129	1,0000
			VR7	0,0072	0,0115	1,0000
			VR8B	0,0039	0,0119	1,0000
			VR8C	-0,0098	0,0125	1,0000
		VA7A	LUM1	-0,0217	0,0192	1,0000
			VA1A	0,0011	0,0142	1,0000
			VA3D	0,0048	0,0142	1,0000
			VA3F	0,0100	0,0144	1,0000
			VA7B	-0,0056	0,0144	1,0000
			VA7C	-0,0044	0,0129	1,0000
			VR7	0,0172	0,0115	0,9980
			VR8B	0,0139	0,0119	1,0000
			VR8C	0,0002	0,0125	1,0000

Width M1 continued

		Localities	Localities	Mean Difference	Standard error	Significance
WITDTH M1	Hochberg	VA7B	LUM1	-0,0162	0,0192	1,0000
			VA1A	0,0067	0,0142	1,0000
			VA3D	0,0104	0,0142	1,0000
			VA3F	0,0156	0,0144	1,0000
			VA7A	0,0056	0,0144	1,0000
			VA7C	0,0011	0,0129	1,0000
			VR7	0,0228	0,0115	0,8848
			VR8B	0,0194	0,0119	0,9910
			VR8C	0,0058	0,0125	1,0000
		VA7C	LUM1	-0,0173	0,0181	1,0000
			VA1A	0,0055	0,0127	1,0000
			VA3D	0,0092	0,0127	1,0000
			VA3F	0,0144	0,0129	1,0000
			VA7A	0,0044	0,0129	1,0000
			VA7B	-0,0011	0,0129	1,0000
			VR7	0,0216	0,0097	0,6848
			VR8B	0,0183	0,0102	0,9614
			VR8C	0,0046	0,0109	1,0000
		VR7	LUM1	-0,0390	0,0172	0,6512
			VA1A	-0,0161	0,0113	0,9992
			VA3D	-0,0124	0,0113	1,0000
			VA3F	-0,0072	0,0115	1,0000
			VA7A	-0,0172	0,0115	0,9980
			VA7B	-0,0228	0,0115	0,8848
			VA7C	-0,0216	0,0097	0,6848
			VR8B	-0,0034	0,0083	1,0000
			VR8C	-0,0170	0,0092	0,9443
		VR8B	LUM1	-0,0356	0,0174	0,8434
			VA1A	-0,0128	0,0117	1,0000
			VA3D	-0,0091	0,0117	1,0000
			VA3F	-0,0039	0,0119	1,0000
			VA7A	-0,0139	0,0119	1,0000
			VA7B	-0,0194	0,0119	0,9910
			VA7C	-0,0183	0,0102	0,9614
			VR7	0,0034	0,0083	1,0000
			VR8C	-0,0136	0,0097	0,9994
		VR8C	LUM1	-0,0220	0,0179	1,0000
			VA1A	0,0009	0,0123	1,0000
			VA3D	0,0046	0,0123	1,0000
			VA3F	0,0098	0,0125	1,0000
			VA7A	-0,0002	0,0125	1,0000
			VA7B	-0,0058	0,0125	1,0000
			VA7C	-0,0046	0,0109	1,0000
			VR7	0,0170	0,0092	0,9443
			VR8B	0,0136	0,0097	0,9994

Table 7. Post hoc of the upper second molars of *Megacricetodon collongensis*. Both for the length and width of the M2, we carried out Hochberg's GT2 due to the equal variances assumed.

		Localities	Localities	Mean Difference	Standard error	Significance
LENGTH M2	Hochberg	LUM1	VA1A	-0,0164	0,0220	1,0000
			VA3D	0,0365	0,0160	0,7777
			VA3F	0,0257	0,0182	1,0000
			VA7A	-0,0033	0,0230	1,0000
			VA7B	0,0105	0,0173	1,0000
			VA7C	-0,0030	0,0173	1,0000
			VA8B	0,0067	0,0230	1,0000
			VA8C	0,0050	0,0230	1,0000
			VR7	0,0205	0,0153	1,0000
			VR8B	0,0350	0,0157	0,8128
			VR8C	0,0104	0,0164	1,0000
		VA1A	LUM1	0,0164	0,0220	1,0000
			VA3D	0,0529	0,0185	0,2575
			VA3F	0,0421	0,0204	0,9202
			VA7A	0,0131	0,0248	1,0000
			VA7B	0,0269	0,0196	1,0000
			VA7C	0,0134	0,0196	1,0000
			VA8B	0,0231	0,0248	1,0000
			VA8C	0,0214	0,0248	1,0000
			VR7	0,0370	0,0179	0,9175
			VR8B	0,0514	0,0182	0,2802
			VR8C	0,0268	0,0188	1,0000
		VA3D	LUM1	-0,0365	0,0160	0,7777
			VA1A	-0,0529	0,0185	0,2575
			VA3F	-0,0108	0,0138	1,0000
			VA7A	-0,0398	0,0197	0,9405
			VA7B	-0,0260	0,0126	0,9181
			VA7C	-0,0395	0,0126	0,1155
			VA8B	-0,0298	0,0197	0,9998
			VA8C	-0,0315	0,0197	0,9993
			VR7	-0,0159	0,0097	0,9985
			VR8B	-0,0015	0,0103	1,0000
			VR8C	-0,0261	0,0114	0,7595
		VA3F	LUM1	-0,0257	0,0182	1,0000
			VA1A	-0,0421	0,0204	0,9202
			VA3D	0,0108	0,0138	1,0000
			VA7A	-0,0290	0,0215	1,0000
			VA7B	-0,0152	0,0152	1,0000
			VA7C	-0,0287	0,0152	0,9785
			VA8B	-0,0190	0,0215	1,0000
			VA8C	-0,0207	0,0215	1,0000
			VR7	-0,0051	0,0130	1,0000
			VR8B	0,0093	0,0134	1,0000
			VR8C	-0,0153	0,0143	1,0000
		VA7A	LUM1	0,0033	0,0230	1,0000
			VA1A	-0,0131	0,0248	1,0000
			VA3D	0,0398	0,0197	0,9405
			VA3F	0,0290	0,0215	1,0000
			VA7B	0,0138	0,0207	1,0000
			VA7C	0,0003	0,0207	1,0000
			VA8B	0,0100	0,0257	1,0000
			VA8C	0,0083	0,0257	1,0000
			VR7	0,0239	0,0191	1,0000
			VR8B	0,0383	0,0195	0,9569
			VR8C	0,0137	0,0200	1,0000

Length M2 continued

		Localities	Localities	Mean Difference	Standard error	Significance
LENGTH M2	Hochberg	VA7B	LUM1	-0,0105	0,0173	1,0000
			VA1A	-0,0269	0,0196	1,0000
			VA3D	0,0260	0,0126	0,9181
			VA3F	0,0152	0,0152	1,0000
			VA7A	-0,0138	0,0207	1,0000
			VA7C	-0,0135	0,0141	1,0000
			VA8B	-0,0038	0,0207	1,0000
			VA8C	-0,0055	0,0207	1,0000
			VR7	0,0100	0,0116	1,0000
			VR8B	0,0245	0,0121	0,9379
			VR8C	-0,0001	0,0130	1,0000
		VA7C	LUM1	0,0030	0,0173	1,0000
			VA1A	-0,0134	0,0196	1,0000
			VA3D	0,0395	0,0126	0,1155
			VA3F	0,0287	0,0152	0,9785
			VA7A	-0,0003	0,0207	1,0000
			VA7B	0,0135	0,0141	1,0000
			VA8B	0,0097	0,0207	1,0000
			VA8C	0,0080	0,0207	1,0000
			VR7	0,0235	0,0116	0,9364
			VR8B	0,0380	0,0121	0,1170
			VR8C	0,0134	0,0130	1,0000
		VA8B	LUM1	-0,0067	0,0230	1,0000
			VA1A	-0,0231	0,0248	1,0000
			VA3D	0,0298	0,0197	0,9998
			VA3F	0,0190	0,0215	1,0000
			VA7A	-0,0100	0,0257	1,0000
			VA7B	0,0038	0,0207	1,0000
			VA7C	-0,0097	0,0207	1,0000
			VA8C	-0,0017	0,0257	1,0000
			VR7	0,0139	0,0191	1,0000
			VR8B	0,0283	0,0195	0,9999
			VR8C	0,0037	0,0200	1,0000
		VA8C	LUM1	-0,0050	0,0230	1,0000
			VA1A	-0,0214	0,0248	1,0000
			VA3D	0,0315	0,0197	0,9993
			VA3F	0,0207	0,0215	1,0000
			VA7A	-0,0083	0,0257	1,0000
			VA7B	0,0055	0,0207	1,0000
			VA7C	-0,0080	0,0207	1,0000
			VA8B	0,0017	0,0257	1,0000
			VR7	0,0155	0,0191	1,0000
			VR8B	0,0300	0,0195	0,9997
			VR8C	0,0054	0,0200	1,0000
		VR7	LUM1	-0,0205	0,0153	1,0000
			VA1A	-0,0370	0,0179	0,9175
			VA3D	0,0159	0,0097	0,9985
			VA3F	0,0051	0,0130	1,0000
			VA7A	-0,0239	0,0191	1,0000
			VA7B	-0,0100	0,0116	1,0000
			VA7C	-0,0235	0,0116	0,9364
			VA8B	-0,0139	0,0191	1,0000
			VA8C	-0,0155	0,0191	1,0000
			VR8B	0,0145	0,0091	0,9993
			VR8C	-0,0102	0,0103	1,0000
		VR8B	LUM1	-0,0350	0,0157	0,8128
			VA1A	-0,0514	0,0182	0,2802
			VA3D	0,0015	0,0103	1,0000
			VA3F	-0,0093	0,0134	1,0000
			VA7A	-0,0383	0,0195	0,9569
			VA7B	-0,0245	0,0121	0,9379
			VA7C	-0,0380	0,0121	0,1170
			VA8B	-0,0283	0,0195	0,9999
			VA8C	-0,0300	0,0195	0,9997
			VR7	-0,0145	0,0091	0,9993
			VR8C	-0,0246	0,0109	0,7848
		VR8C	LUM1	-0,0104	0,0164	1,0000
			VA1A	-0,0268	0,0188	1,0000
			VA3D	0,0261	0,0114	0,7595
			VA3F	0,0153	0,0143	1,0000
			VA7A	-0,0137	0,0200	1,0000
			VA7B	0,0001	0,0130	1,0000
			VA7C	-0,0134	0,0130	1,0000
			VA8B	-0,0037	0,0200	1,0000
			VA8C	-0,0054	0,0200	1,0000
			VR7	0,0102	0,0103	1,0000
			VR8B	0,0246	0,0109	0,7848

		Localities	Localities	Mean Difference	Standard error	Significance
WITDTH M2	Hochberg	LUM1	VA1A	0,0133	0,0180	1,0000
			VA3D	0,0591	0,0136	0,0014
			VA3F	0,0504	0,0148	0,0485
			VA7A	0,0206	0,0187	1,0000
			VA7B	0,0368	0,0145	0,5378
			VA7C	0,0112	0,0142	1,0000
			VA8B	0,0353	0,0195	0,9895
			VA8C	0,0220	0,0207	1,0000
			VR7	0,0600	0,0130	0,0004
			VR8B	0,0525	0,0133	0,0070
			VR8C	0,0363	0,0139	0,4664
		VA1A	LUM1	-0,0133	0,0180	1,0000
			VA3D	0,0458	0,0149	0,1391
			VA3F	0,0372	0,0160	0,7291
			VA7A	0,0073	0,0196	1,0000
			VA7B	0,0235	0,0157	0,9999
			VA7C	-0,0021	0,0155	1,0000
			VA8B	0,0221	0,0204	1,0000
			VA8C	0,0087	0,0216	1,0000
			VR7	0,0468	0,0143	0,0770
			VR8B	0,0392	0,0146	0,3902
			VR8C	0,0230	0,0152	0,9998
		VA3D	LUM1	-0,0591	0,0136	0,0014
			VA1A	-0,0458	0,0149	0,1391
			VA3F	-0,0086	0,0108	1,0000
			VA7A	-0,0385	0,0157	0,6145
			VA7B	-0,0223	0,0105	0,8888
			VA7C	-0,0479	0,0101	0,0002
			VA8B	-0,0237	0,0168	1,0000
			VA8C	-0,0371	0,0181	0,9294
			VR7	0,0010	0,0082	1,0000
			VR8B	-0,0066	0,0087	1,0000
			VR8C	-0,0228	0,0097	0,7036
		VA3F	LUM1	-0,0504	0,0148	0,0485
			VA1A	-0,0372	0,0160	0,7291
			VA3D	0,0086	0,0108	1,0000
			VA7A	-0,0298	0,0167	0,9918
			VA7B	-0,0137	0,0120	1,0000
			VA7C	-0,0393	0,0116	0,0541
			VA8B	-0,0151	0,0177	1,0000
			VA8C	-0,0284	0,0190	0,9999
			VR7	0,0096	0,0100	1,0000
			VR8B	0,0021	0,0105	1,0000
			VR8C	-0,0141	0,0113	1,0000
		VA7A	LUM1	-0,0206	0,0187	1,0000
			VA1A	-0,0073	0,0196	1,0000
			VA3D	0,0385	0,0157	0,6145
			VA3F	0,0298	0,0167	0,9918
			VA7B	0,0162	0,0165	1,0000
			VA7C	-0,0094	0,0163	1,0000
			VA8B	0,0148	0,0211	1,0000
			VA8C	0,0014	0,0222	1,0000
			VR7	0,0395	0,0152	0,4678
			VR8B	0,0319	0,0155	0,9199
			VR8C	0,0157	0,0160	1,0000
		VA7B	LUM1	-0,0368	0,0145	0,5378
			VA1A	-0,0235	0,0157	0,9999
			VA3D	0,0223	0,0105	0,8888
			VA3F	0,0137	0,0120	1,0000
			VA7A	-0,0162	0,0165	1,0000
			VA7C	-0,0256	0,0113	0,7878
			VA8B	-0,0014	0,0175	1,0000
			VA8C	-0,0148	0,0188	1,0000
			VR7	0,0233	0,0097	0,6603
			VR8B	0,0157	0,0101	0,9996
			VR8C	-0,0005	0,0109	1,0000

Width M2 continued

		Localities	Localities	Mean Difference	Standard error	Significance
WITDTH M2	Hochberg	VA7C	LUM1	-0,0112	0,0142	1,0000
			VA1A	0,0021	0,0155	1,0000
			VA3D	0,0479	0,0101	0,0002
			VA3F	0,0393	0,0116	0,0541
			VA7A	0,0094	0,0163	1,0000
			VA7B	0,0256	0,0113	0,7878
			VA8B	0,0242	0,0173	1,0000
			VA8C	0,0108	0,0186	1,0000
			VR7	0,0489	0,0092	0,0000
			VR8B	0,0413	0,0097	0,0019
			VR8C	0,0251	0,0105	0,6770
		VA8B	LUM1	-0,0353	0,0195	0,9895
			VA1A	-0,0221	0,0204	1,0000
			VA3D	0,0237	0,0168	1,0000
			VA3F	0,0151	0,0177	1,0000
			VA7A	-0,0148	0,0211	1,0000
			VA7B	0,0014	0,0175	1,0000
			VA7C	-0,0242	0,0173	1,0000
			VA8C	-0,0133	0,0229	1,0000
			VR7	0,0247	0,0163	0,9998
			VR8B	0,0171	0,0165	1,0000
			VR8C	0,0010	0,0170	1,0000
		VA8C	LUM1	-0,0220	0,0207	1,0000
			VA1A	-0,0087	0,0216	1,0000
			VA3D	0,0371	0,0181	0,9294
			VA3F	0,0284	0,0190	0,9999
			VA7A	-0,0014	0,0222	1,0000
			VA7B	0,0148	0,0188	1,0000
			VA7C	-0,0108	0,0186	1,0000
			VA8B	0,0133	0,0229	1,0000
			VR7	0,0380	0,0177	0,8699
			VR8B	0,0305	0,0179	0,9968
			VR8C	0,0143	0,0184	1,0000
		VR7	LUM1	-0,0600	0,0130	0,0004
			VA1A	-0,0468	0,0143	0,0770
			VA3D	-0,0010	0,0082	1,0000
			VA3F	-0,0096	0,0100	1,0000
			VA7A	-0,0395	0,0152	0,4678
			VA7B	-0,0233	0,0097	0,6603
			VA7C	-0,0489	0,0092	0,0000
			VA8B	-0,0247	0,0163	0,9998
			VA8C	-0,0380	0,0177	0,8699
			VR8B	-0,0076	0,0077	1,0000
			VR8C	-0,0238	0,0088	0,3693
		VR8B	LUM1	-0,0525	0,0133	0,0070
			VA1A	-0,0392	0,0146	0,3902
			VA3D	0,0066	0,0087	1,0000
			VA3F	-0,0021	0,0105	1,0000
			VA7A	-0,0319	0,0155	0,9199
			VA7B	-0,0157	0,0101	0,9996
			VA7C	-0,0413	0,0097	0,0019
			VA8B	-0,0171	0,0165	1,0000
			VA8C	-0,0305	0,0179	0,9968
			VR7	0,0076	0,0077	1,0000
			VR8C	-0,0162	0,0092	0,9941
		VR8C	LUM1	-0,0363	0,0139	0,4664
			VA1A	-0,0230	0,0152	0,9998
			VA3D	0,0228	0,0097	0,7036
			VA3F	0,0141	0,0113	1,0000
			VA7A	-0,0157	0,0160	1,0000
			VA7B	0,0005	0,0109	1,0000
			VA7C	-0,0251	0,0105	0,6770
			VA8B	-0,0010	0,0170	1,0000
			VA8C	-0,0143	0,0184	1,0000
			VR7	0,0238	0,0088	0,3693
			VR8B	0,0162	0,0092	0,9941

APPENDIX 6.3

Analysis of variance (One-Way ANOVA) for the assemblages of *Megacricetodon gersii* from the Calatayud-Montalbán Basin.
All analyses were accomplished using exclusively localities with sample sizes larger than five specimens.
Values in red are those where the difference between the means are significant at 0.5.

Table 1. Levene's test of the lower and upper molars of *Megacricetodon gersii.*

		Levene's test	gl1	gl2	Significance
m1	Length	1,012	17	211	0,446
	Width	2,459	16	302	0,002
m2	Length	1,51	19	281	0,081
	Width	0,823	17	293	0,666
M1	Length	2,522	17	224	0,001
	Width	1,9	17	285	0,018
M2	Length	2,82	18	254	0,000
	Width	1,075	18	269	0,378

Table 2. In the cases that there is homogeneity of variance, we carried out One-Way ANOVA.

		F	Significance
m1	Length	3,387	0,000
m2	Length	2,152	0,004
	Width	4,182	0
M2	Width	2,933	0,000

Table 3. In the cases that there is not homogeneity of variance, we carried out Welch and Brown-Forsythe.

			Estadistic	gl1	gl2	Significance
m1	Width	Welch	2,291	16	80,156	0,008
		Brown-Forsythe	2,44	16	158,96	0,003
M1	Length	Welch	3,733	17	55,358	0,000
		Brown-Forsythe	2,494	17	104,28	0,002
	Width	Welch	6,095	17	67,774	0,000
		Brown-Forsythe	4,715	17	141,19	0,000
M2	Length	Welch	3	18	61,613	0,001
		Brown-Forsythe	2,457	18	99,242	0,003

Table 4. Post hoc of the m1 of *Megacricetodon gersii*. For the length, we carried out Hochberg's GT2; and for the width we carried out Games-Howell.

		Localities	Localities	Mean Difference	Standard error	Significance
LENGTH m1	Hochberg	LP4BA	LUM10	0,0129	0,0211	1,0000
			LUM11	0,0245	0,0148	1,0000
			LUM12	0,0585	0,0177	0,1540
			LUM14	0,0673	0,0189	0,0682
			LUM16	0,0568	0,0175	0,1819
			LUM17	0,0535	0,0189	0,5265
			LUM18	0,0448	0,0281	1,0000
			LUM19	0,0215	0,0177	1,0000
			LUM20	0,0273	0,0186	1,0000
			LUM3	0,0693	0,0258	0,6692
			LUM4	0,0645	0,0229	0,5325
			LUM7	0,0033	0,0258	1,0000
			LUM8	0,0102	0,0229	1,0000
			LUM9	0,0581	0,0189	0,3015
			VA7D	0,1040	0,0316	0,1610
			VA7E	0,0716	0,0186	0,0231
			VA7F	0,0957	0,0242	0,0154
		LUM10	LP4BA	-0,0129	0,0211	1,0000
			LUM11	0,0116	0,0181	1,0000
			LUM12	0,0456	0,0206	0,9768
			LUM14	0,0544	0,0217	0,8304
			LUM16	0,0439	0,0204	0,9874
			LUM17	0,0406	0,0217	0,9997
			LUM18	0,0319	0,0301	1,0000
			LUM19	0,0086	0,0206	1,0000
			LUM20	0,0144	0,0214	1,0000
			LUM3	0,0564	0,0279	0,9972
			LUM4	0,0516	0,0252	0,9962
			LUM7	-0,0096	0,0279	1,0000
			LUM8	-0,0027	0,0252	1,0000
			LUM9	0,0452	0,0217	0,9939
			VA7D	0,0911	0,0333	0,6197
			VA7E	0,0587	0,0214	0,6031
			VA7F	0,0828	0,0264	0,2470
		LUM11	LP4BA	-0,0245	0,0148	1,0000
			LUM10	-0,0116	0,0181	1,0000
			LUM12	0,0340	0,0141	0,8956
			LUM14	0,0429	0,0156	0,6050
			LUM16	0,0323	0,0138	0,9346
			LUM17	0,0290	0,0156	0,9998
			LUM18	0,0204	0,0260	1,0000
			LUM19	-0,0030	0,0141	1,0000
			LUM20	0,0029	0,0152	1,0000
			LUM3	0,0449	0,0235	0,9995
			LUM4	0,0400	0,0202	0,9985
			LUM7	-0,0211	0,0235	1,0000
			LUM8	-0,0143	0,0202	1,0000
			LUM9	0,0336	0,0156	0,9867
			VA7D	0,0795	0,0297	0,6805
			VA7E	0,0471	0,0152	0,2680
			VA7F	0,0712	0,0216	0,1595
		LUM12	LP4BA	-0,0585	0,0177	0,1540
			LUM10	-0,0456	0,0206	0,9768
			LUM11	-0,0340	0,0141	0,8956
			LUM14	0,0088	0,0184	1,0000
			LUM16	-0,0017	0,0169	1,0000
			LUM17	-0,0050	0,0184	1,0000
			LUM18	-0,0137	0,0278	1,0000
			LUM19	-0,0371	0,0172	0,9860
			LUM20	-0,0312	0,0180	1,0000
			LUM3	0,0108	0,0254	1,0000
			LUM4	0,0060	0,0225	1,0000
			LUM7	-0,0552	0,0254	0,9847
			LUM8	-0,0483	0,0225	0,9872
			LUM9	-0,0004	0,0184	1,0000
			VA7D	0,0455	0,0313	1,0000
			VA7E	0,0131	0,0180	1,0000
			VA7F	0,0372	0,0237	1,0000

Length m1 continued

		Localities	Localities	Mean Difference	Standard error	Significance
LENGTH m1	Hochberg	LUM14	LP4BA	-0,0673	0,0189	0,0682
			LUM10	-0,0544	0,0217	0,8304
			LUM11	-0,0429	0,0156	0,6050
			LUM12	-0,0088	0,0184	1,0000
			LUM16	-0,0106	0,0182	1,0000
			LUM17	-0,0138	0,0196	1,0000
			LUM18	-0,0225	0,0286	1,0000
			LUM19	-0,0459	0,0184	0,8462
			LUM20	-0,0400	0,0193	0,9944
			LUM3	0,0020	0,0263	1,0000
			LUM4	-0,0029	0,0234	1,0000
			LUM7	-0,0640	0,0263	0,8868
			LUM8	-0,0571	0,0234	0,8833
			LUM9	-0,0092	0,0196	1,0000
			VA7D	0,0367	0,0320	1,0000
			VA7E	0,0043	0,0193	1,0000
			VA7F	0,0283	0,0247	1,0000
		LUM16	LP4BA	-0,0568	0,0175	0,1819
			LUM10	-0,0439	0,0204	0,9874
			LUM11	-0,0323	0,0138	0,9346
			LUM12	0,0017	0,0169	1,0000
			LUM14	0,0106	0,0182	1,0000
			LUM17	-0,0033	0,0182	1,0000
			LUM18	-0,0119	0,0276	1,0000
			LUM19	-0,0353	0,0169	0,9936
			LUM20	-0,0294	0,0178	1,0000
			LUM3	0,0126	0,0253	1,0000
			LUM4	0,0077	0,0223	1,0000
			LUM7	-0,0534	0,0253	0,9914
			LUM8	-0,0466	0,0223	0,9934
			LUM9	0,0013	0,0182	1,0000
			VA7D	0,0472	0,0312	1,0000
			VA7E	0,0148	0,0178	1,0000
			VA7F	0,0389	0,0236	1,0000
		LUM17	LP4BA	-0,0535	0,0189	0,5265
			LUM10	-0,0406	0,0217	0,9997
			LUM11	-0,0290	0,0156	0,9998
			LUM12	0,0050	0,0184	1,0000
			LUM14	0,0138	0,0196	1,0000
			LUM16	0,0033	0,0182	1,0000
			LUM18	-0,0087	0,0286	1,0000
			LUM19	-0,0320	0,0184	1,0000
			LUM20	-0,0262	0,0193	1,0000
			LUM3	0,0158	0,0263	1,0000
			LUM4	0,0110	0,0234	1,0000
			LUM7	-0,0502	0,0263	0,9995
			LUM8	-0,0433	0,0234	0,9998
			LUM9	0,0046	0,0196	1,0000
			VA7D	0,0505	0,0320	1,0000
			VA7E	0,0181	0,0193	1,0000
			VA7F	0,0422	0,0247	1,0000
		LUM18	LP4BA	-0,0448	0,0281	1,0000
			LUM10	-0,0319	0,0301	1,0000
			LUM11	-0,0204	0,0260	1,0000
			LUM12	0,0137	0,0278	1,0000
			LUM14	0,0225	0,0286	1,0000
			LUM16	0,0119	0,0276	1,0000
			LUM17	0,0087	0,0286	1,0000
			LUM19	-0,0234	0,0278	1,0000
			LUM20	-0,0175	0,0284	1,0000
			LUM3	0,0245	0,0335	1,0000
			LUM4	0,0196	0,0313	1,0000
			LUM7	-0,0415	0,0335	1,0000
			LUM8	-0,0346	0,0313	1,0000
			LUM9	0,0133	0,0286	1,0000
			VA7D	0,0592	0,0382	1,0000
			VA7E	0,0268	0,0284	1,0000
			VA7F	0,0508	0,0323	1,0000

Length m1 continued

		Localities	Localities	Mean Difference	Standard error	Significance
LENGTH m1	Hochberg	LUM19	LP4BA	-0,0215	0,0177	1,0000
			LUM10	-0,0086	0,0206	1,0000
			LUM11	0,0030	0,0141	1,0000
			LUM12	0,0371	0,0172	0,9860
			LUM14	0,0459	0,0184	0,8462
			LUM16	0,0353	0,0169	0,9936
			LUM17	0,0320	0,0184	1,0000
			LUM18	0,0234	0,0278	1,0000
			LUM20	0,0059	0,0180	1,0000
			LUM3	0,0479	0,0254	0,9997
			LUM4	0,0430	0,0225	0,9994
			LUM7	-0,0181	0,0254	1,0000
			LUM8	-0,0113	0,0225	1,0000
			LUM9	0,0367	0,0184	0,9982
			VA7D	0,0825	0,0313	0,7181
			VA7E	0,0502	0,0180	0,5709
			VA7F	0,0742	0,0237	0,2576
		LUM20	LP4BA	-0,0273	0,0186	1,0000
			LUM10	-0,0144	0,0214	1,0000
			LUM11	-0,0029	0,0152	1,0000
			LUM12	0,0312	0,0180	1,0000
			LUM14	0,0400	0,0193	0,9944
			LUM16	0,0294	0,0178	1,0000
			LUM17	0,0262	0,0193	1,0000
			LUM18	0,0175	0,0284	1,0000
			LUM19	-0,0059	0,0180	1,0000
			LUM3	0,0420	0,0261	1,0000
			LUM4	0,0371	0,0231	1,0000
			LUM7	-0,0240	0,0261	1,0000
			LUM8	-0,0171	0,0231	1,0000
			LUM9	0,0308	0,0193	1,0000
			VA7D	0,0767	0,0318	0,9004
			VA7E	0,0443	0,0189	0,9349
			VA7F	0,0683	0,0244	0,5494
		LUM3	LP4BA	-0,0693	0,0258	0,6692
			LUM10	-0,0564	0,0279	0,9972
			LUM11	-0,0449	0,0235	0,9995
			LUM12	-0,0108	0,0254	1,0000
			LUM14	-0,0020	0,0263	1,0000
			LUM16	-0,0126	0,0253	1,0000
			LUM17	-0,0158	0,0263	1,0000
			LUM18	-0,0245	0,0335	1,0000
			LUM19	-0,0479	0,0254	0,9997
			LUM20	-0,0420	0,0261	1,0000
			LUM4	-0,0049	0,0293	1,0000
			LUM7	-0,0660	0,0316	0,9937
			LUM8	-0,0591	0,0293	0,9973
			LUM9	-0,0112	0,0263	1,0000
			VA7D	0,0347	0,0365	1,0000
			VA7E	0,0023	0,0261	1,0000
			VA7F	0,0263	0,0303	1,0000
		LUM4	LP4BA	-0,0645	0,0229	0,5325
			LUM10	-0,0516	0,0252	0,9962
			LUM11	-0,0400	0,0202	0,9985
			LUM12	-0,0060	0,0225	1,0000
			LUM14	0,0029	0,0234	1,0000
			LUM16	-0,0077	0,0223	1,0000
			LUM17	-0,0110	0,0234	1,0000
			LUM18	-0,0196	0,0313	1,0000
			LUM19	-0,0430	0,0225	0,9994
			LUM20	-0,0371	0,0231	1,0000
			LUM3	0,0049	0,0293	1,0000
			LUM7	-0,0611	0,0293	0,9936
			LUM8	-0,0543	0,0267	0,9969
			LUM9	-0,0064	0,0234	1,0000
			VA7D	0,0395	0,0345	1,0000
			VA7E	0,0071	0,0231	1,0000
			VA7F	0,0312	0,0278	1,0000

Length m1 continued

		Localities	Localities	Mean Difference	Standard error	Significance
LENGTH m1	Hochberg	LUM7	LP4BA	-0,0033	0,0258	1,0000
			LUM10	0,0096	0,0279	1,0000
			LUM11	0,0211	0,0235	1,0000
			LUM12	0,0552	0,0254	0,9847
			LUM14	0,0640	0,0263	0,8868
			LUM16	0,0534	0,0253	0,9914
			LUM17	0,0502	0,0263	0,9995
			LUM18	0,0415	0,0335	1,0000
			LUM19	0,0181	0,0254	1,0000
			LUM20	0,0240	0,0261	1,0000
			LUM3	0,0660	0,0316	0,9937
			LUM4	0,0611	0,0293	0,9936
			LUM8	0,0069	0,0293	1,0000
			LUM9	0,0548	0,0263	0,9941
			VA7D	0,1007	0,0365	0,5952
			VA7E	0,0683	0,0261	0,7327
			VA7F	0,0923	0,0303	0,3150
		LUM8	LP4BA	-0,0102	0,0229	1,0000
			LUM10	0,0027	0,0252	1,0000
			LUM11	0,0143	0,0202	1,0000
			LUM12	0,0483	0,0225	0,9872
			LUM14	0,0571	0,0234	0,8833
			LUM16	0,0466	0,0223	0,9934
			LUM17	0,0433	0,0234	0,9998
			LUM18	0,0346	0,0313	1,0000
			LUM19	0,0113	0,0225	1,0000
			LUM20	0,0171	0,0231	1,0000
			LUM3	0,0591	0,0293	0,9973
			LUM4	0,0543	0,0267	0,9969
			LUM7	-0,0069	0,0293	1,0000
			LUM9	0,0479	0,0234	0,9963
			VA7D	0,0938	0,0345	0,6347
			VA7E	0,0614	0,0231	0,7007
			VA7F	0,0855	0,0278	0,2968
		LUM9	LP4BA	-0,0581	0,0189	0,3015
			LUM10	-0,0452	0,0217	0,9939
			LUM11	-0,0336	0,0156	0,9867
			LUM12	0,0004	0,0184	1,0000
			LUM14	0,0092	0,0196	1,0000
			LUM16	-0,0013	0,0182	1,0000
			LUM17	-0,0046	0,0196	1,0000
			LUM18	-0,0133	0,0286	1,0000
			LUM19	-0,0367	0,0184	0,9982
			LUM20	-0,0308	0,0193	1,0000
			LUM3	0,0112	0,0263	1,0000
			LUM4	0,0064	0,0234	1,0000
			LUM7	-0,0548	0,0263	0,9941
			LUM8	-0,0479	0,0234	0,9963
			VA7D	0,0459	0,0320	1,0000
			VA7E	0,0135	0,0193	1,0000
			VA7F	0,0376	0,0247	1,0000
		VA7D	LP4BA	-0,1040	0,0316	0,1610
			LUM10	-0,0911	0,0333	0,6197
			LUM11	-0,0795	0,0297	0,6805
			LUM12	-0,0455	0,0313	1,0000
			LUM14	-0,0367	0,0320	1,0000
			LUM16	-0,0472	0,0312	1,0000
			LUM17	-0,0505	0,0320	1,0000
			LUM18	-0,0592	0,0382	1,0000
			LUM19	-0,0825	0,0313	0,7181
			LUM20	-0,0767	0,0318	0,9004
			LUM3	-0,0347	0,0365	1,0000
			LUM4	-0,0395	0,0345	1,0000
			LUM7	-0,1007	0,0365	0,5952
			LUM8	-0,0938	0,0345	0,6347
			LUM9	-0,0459	0,0320	1,0000
			VA7E	-0,0324	0,0318	1,0000
			VA7F	-0,0083	0,0354	1,0000

Length m1 continued

		Localities	Localities	Mean Difference	Standard error	Significance
LENGTH m1	Hochberg	VA7E	LP4BA	-0,0716	0,0186	0,0231
			LUM10	-0,0587	0,0214	0,6031
			LUM11	-0,0471	0,0152	0,2680
			LUM12	-0,0131	0,0180	1,0000
			LUM14	-0,0043	0,0193	1,0000
			LUM16	-0,0148	0,0178	1,0000
			LUM17	-0,0181	0,0193	1,0000
			LUM18	-0,0268	0,0284	1,0000
			LUM19	-0,0502	0,0180	0,5709
			LUM20	-0,0443	0,0189	0,9349
			LUM3	-0,0023	0,0261	1,0000
			LUM4	-0,0071	0,0231	1,0000
			LUM7	-0,0683	0,0261	0,7327
			LUM8	-0,0614	0,0231	0,7007
			LUM9	-0,0135	0,0193	1,0000
			VA7D	0,0324	0,0318	1,0000
			VA7F	0,0240	0,0244	1,0000
		VA7F	LP4BA	-0,0957	0,0242	0,0154
			LUM10	-0,0828	0,0264	0,2470
			LUM11	-0,0712	0,0216	0,1595
			LUM12	-0,0372	0,0237	1,0000
			LUM14	-0,0283	0,0247	1,0000
			LUM16	-0,0389	0,0236	1,0000
			LUM17	-0,0422	0,0247	1,0000
			LUM18	-0,0508	0,0323	1,0000
			LUM19	-0,0742	0,0237	0,2576
			LUM20	-0,0683	0,0244	0,5494
			LUM3	-0,0263	0,0303	1,0000
			LUM4	-0,0312	0,0278	1,0000
			LUM7	-0,0923	0,0303	0,3150
			LUM8	-0,0855	0,0278	0,2968
			LUM9	-0,0376	0,0247	1,0000
			VA7D	0,0083	0,0354	1,0000
			VA7E	-0,0240	0,0244	1,0000

Width m1

		Localities	Localities	Mean Difference	Standard error	Significance
WIDTH m1	Games-Howell	LP4BA	LUM10	0,0192	0,0138	0,9851
			LUM11	0,0274	0,0077	0,0647
			LUM12	0,0415	0,0095	0,0073
			LUM14	0,0452	0,0102	0,0059
			LUM16	0,0328	0,0117	0,3292
			LUM17	0,0489	0,0126	0,0397
			LUM18	0,0341	0,0159	0,7403
			LUM19	0,0370	0,0103	0,0611
			LUM20	0,0068	0,0147	1,0000
			LUM3	0,0489	0,0209	0,6330
			LUM4	0,0329	0,0113	0,2883
			LUM7	0,0164	0,0147	0,9975
			LUM8	0,0190	0,0146	0,9930
			LUM9	0,0194	0,0103	0,8843
			VA7E	0,0372	0,0114	0,1342
			VA7F	0,0363	0,0095	0,0489
		LUM10	LP4BA	-0,0192	0,0138	0,9851
			LUM11	0,0082	0,0124	1,0000
			LUM12	0,0223	0,0136	0,9451
			LUM14	0,0260	0,0141	0,8839
			LUM16	0,0136	0,0152	0,9999
			LUM17	0,0297	0,0159	0,8799
			LUM18	0,0149	0,0187	1,0000
			LUM19	0,0178	0,0142	0,9947
			LUM20	-0,0124	0,0176	1,0000
			LUM3	0,0297	0,0231	0,9907
			LUM4	0,0137	0,0149	0,9998
			LUM7	-0,0028	0,0177	1,0000
			LUM8	-0,0002	0,0176	1,0000
			LUM9	0,0002	0,0142	1,0000
			VA7E	0,0180	0,0150	0,9969
			VA7F	0,0171	0,0136	0,9936

Width m1 continued

		Localities	Localities	Mean Difference	Standard error	Significance
WIDTH m1	Games-Howell	LUM11	LP4BA	-0,0274	0,0077	0,0647
			LUM10	-0,0082	0,0124	1,0000
			LUM12	0,0141	0,0074	0,8700
			LUM14	0,0178	0,0082	0,7367
			LUM16	0,0054	0,0100	1,0000
			LUM17	0,0216	0,0111	0,8417
			LUM18	0,0067	0,0148	1,0000
			LUM19	0,0096	0,0084	0,9987
			LUM20	-0,0206	0,0134	0,9702
			LUM3	0,0216	0,0200	0,9971
			LUM4	0,0055	0,0095	1,0000
			LUM7	-0,0109	0,0134	0,9999
			LUM8	-0,0083	0,0133	1,0000
			LUM9	-0,0080	0,0083	0,9998
			VA7E	0,0098	0,0097	0,9996
			VA7F	0,0089	0,0074	0,9952
		LUM12	LP4BA	-0,0415	0,0095	0,0073
			LUM10	-0,0223	0,0136	0,9451
			LUM11	-0,0141	0,0074	0,8700
			LUM14	0,0037	0,0100	1,0000
			LUM16	-0,0087	0,0115	1,0000
			LUM17	0,0074	0,0124	1,0000
			LUM18	-0,0074	0,0158	1,0000
			LUM19	-0,0045	0,0101	1,0000
			LUM20	-0,0347	0,0145	0,5957
			LUM3	0,0074	0,0208	1,0000
			LUM4	-0,0086	0,0111	1,0000
			LUM7	-0,0251	0,0146	0,9148
			LUM8	-0,0225	0,0145	0,9663
			LUM9	-0,0221	0,0101	0,7208
			VA7E	-0,0043	0,0112	1,0000
			VA7F	-0,0052	0,0093	1,0000
		LUM14	LP4BA	-0,0452	0,0102	0,0059
			LUM10	-0,0260	0,0141	0,8839
			LUM11	-0,0178	0,0082	0,7367
			LUM12	-0,0037	0,0100	1,0000
			LUM16	-0,0124	0,0121	0,9997
			LUM17	0,0038	0,0129	1,0000
			LUM18	-0,0111	0,0162	1,0000
			LUM19	-0,0082	0,0108	1,0000
			LUM20	-0,0384	0,0150	0,4814
			LUM3	0,0038	0,0211	1,0000
			LUM4	-0,0123	0,0117	0,9994
			LUM7	-0,0287	0,0150	0,8468
			LUM8	-0,0262	0,0149	0,9199
			LUM9	-0,0258	0,0107	0,5787
			VA7E	-0,0080	0,0118	1,0000
			VA7F	-0,0089	0,0100	0,9999
		LUM16	LP4BA	-0,0328	0,0117	0,3292
			LUM10	-0,0136	0,0152	0,9999
			LUM11	-0,0054	0,0100	1,0000
			LUM12	0,0087	0,0115	1,0000
			LUM14	0,0124	0,0121	0,9997
			LUM17	0,0161	0,0141	0,9988
			LUM18	0,0013	0,0172	1,0000
			LUM19	0,0042	0,0122	1,0000
			LUM20	-0,0260	0,0160	0,9613
			LUM3	0,0161	0,0219	1,0000
			LUM4	0,0001	0,0130	1,0000
			LUM7	-0,0164	0,0161	0,9993
			LUM8	-0,0138	0,0160	0,9999
			LUM9	-0,0134	0,0121	0,9992
			VA7E	0,0044	0,0131	1,0000
			VA7F	0,0035	0,0115	1,0000
		LUM17	LP4BA	-0,0489	0,0126	0,0397
			LUM10	-0,0297	0,0159	0,8799
			LUM11	-0,0216	0,0111	0,8417
			LUM12	-0,0074	0,0124	1,0000
			LUM14	-0,0038	0,0129	1,0000
			LUM16	-0,0161	0,0141	0,9988
			LUM18	-0,0149	0,0178	0,9999
			LUM19	-0,0119	0,0131	0,9999
			LUM20	-0,0422	0,0167	0,5042
			LUM3	0,0000	0,0224	1,0000
			LUM4	-0,0161	0,0138	0,9983
			LUM7	-0,0325	0,0167	0,8425
			LUM8	-0,0299	0,0166	0,9099
			LUM9	-0,0295	0,0130	0,6697
			VA7E	-0,0117	0,0139	1,0000
			VA7F	-0,0126	0,0124	0,9996

Width m1 continued

		Localities	Localities	Mean Difference	Standard error	Significance
WIDTH m1	Games-Howell	LUM18	LP4BA	-0,0341	0,0159	0,7403
			LUM10	-0,0149	0,0187	1,0000
			LUM11	-0,0067	0,0148	1,0000
			LUM12	0,0074	0,0158	1,0000
			LUM14	0,0111	0,0162	1,0000
			LUM16	-0,0013	0,0172	1,0000
			LUM17	0,0149	0,0178	0,9999
			LUM19	0,0029	0,0163	1,0000
			LUM20	-0,0273	0,0194	0,9858
			LUM3	0,0149	0,0244	1,0000
			LUM4	-0,0012	0,0169	1,0000
			LUM7	-0,0176	0,0194	0,9998
			LUM8	-0,0150	0,0193	1,0000
			LUM9	-0,0147	0,0163	0,9998
			VA7E	0,0031	0,0170	1,0000
			VA7F	0,0022	0,0158	1,0000
		LUM19	LP4BA	-0,0370	0,0103	0,0611
			LUM10	-0,0178	0,0142	0,9947
			LUM11	-0,0096	0,0084	0,9987
			LUM12	0,0045	0,0101	1,0000
			LUM14	0,0082	0,0108	1,0000
			LUM16	-0,0042	0,0122	1,0000
			LUM17	0,0119	0,0131	0,9999
			LUM18	-0,0029	0,0163	1,0000
			LUM20	-0,0302	0,0151	0,8261
			LUM3	0,0119	0,0212	1,0000
			LUM4	-0,0041	0,0118	1,0000
			LUM7	-0,0206	0,0151	0,9858
			LUM8	-0,0180	0,0150	0,9972
			LUM9	-0,0176	0,0108	0,9627
			VA7E	0,0002	0,0119	1,0000
			VA7F	-0,0007	0,0101	1,0000
		LUM20	LP4BA	-0,0068	0,0147	1,0000
			LUM10	0,0124	0,0176	1,0000
			LUM11	0,0206	0,0134	0,9702
			LUM12	0,0347	0,0145	0,5957
			LUM14	0,0384	0,0150	0,4814
			LUM16	0,0260	0,0160	0,9613
			LUM17	0,0422	0,0167	0,5042
			LUM18	0,0273	0,0194	0,9858
			LUM19	0,0302	0,0151	0,8261
			LUM3	0,0422	0,0236	0,8989
			LUM4	0,0261	0,0157	0,9519
			LUM7	0,0097	0,0184	1,0000
			LUM8	0,0123	0,0183	1,0000
			LUM9	0,0126	0,0150	1,0000
			VA7E	0,0304	0,0158	0,8654
			VA7F	0,0295	0,0145	0,8079
		LUM3	LP4BA	-0,0489	0,0209	0,6330
			LUM10	-0,0297	0,0231	0,9907
			LUM11	-0,0216	0,0200	0,9971
			LUM12	-0,0074	0,0208	1,0000
			LUM14	-0,0038	0,0211	1,0000
			LUM16	-0,0161	0,0219	1,0000
			LUM17	0,0000	0,0224	1,0000
			LUM18	-0,0149	0,0244	1,0000
			LUM19	-0,0119	0,0212	1,0000
			LUM20	-0,0422	0,0236	0,8989
			LUM4	-0,0161	0,0217	1,0000
			LUM7	-0,0325	0,0236	0,9841
			LUM8	-0,0299	0,0236	0,9925
			LUM9	-0,0295	0,0211	0,9779
			VA7E	-0,0117	0,0217	1,0000
			VA7F	-0,0126	0,0208	1,0000
		LUM4	LP4BA	-0,0329	0,0113	0,2883
			LUM10	-0,0137	0,0149	0,9998
			LUM11	-0,0055	0,0095	1,0000
			LUM12	0,0086	0,0111	1,0000
			LUM14	0,0123	0,0117	0,9994
			LUM16	-0,0001	0,0130	1,0000
			LUM17	0,0161	0,0138	0,9983
			LUM18	0,0012	0,0169	1,0000
			LUM19	0,0041	0,0118	1,0000
			LUM20	-0,0261	0,0157	0,9519
			LUM3	0,0161	0,0217	1,0000
			LUM7	-0,0164	0,0158	0,9990
			LUM8	-0,0138	0,0157	0,9999
			LUM9	-0,0135	0,0117	0,9985
			VA7E	0,0043	0,0127	1,0000
			VA7F	0,0034	0,0111	1,0000

Width m1 continued

		Localities	Localities	Mean Difference	Standard error	Significance
WIDTH m1	Games-Howell	LUM7	LP4BA	-0,0164	0,0147	0,9975
			LUM10	0,0028	0,0177	1,0000
			LUM11	0,0109	0,0134	0,9999
			LUM12	0,0251	0,0146	0,9148
			LUM14	0,0287	0,0150	0,8468
			LUM16	0,0164	0,0161	0,9993
			LUM17	0,0325	0,0167	0,8425
			LUM18	0,0176	0,0194	0,9998
			LUM19	0,0206	0,0151	0,9858
			LUM20	-0,0097	0,0184	1,0000
			LUM3	0,0325	0,0236	0,9841
			LUM4	0,0164	0,0158	0,9990
			LUM8	0,0026	0,0183	1,0000
			LUM9	0,0030	0,0151	1,0000
			VA7E	0,0208	0,0159	0,9909
			VA7F	0,0199	0,0146	0,9835
		LUM8	LP4BA	-0,0190	0,0146	0,9930
			LUM10	0,0002	0,0176	1,0000
			LUM11	0,0083	0,0133	1,0000
			LUM12	0,0225	0,0145	0,9663
			LUM14	0,0262	0,0149	0,9199
			LUM16	0,0138	0,0160	0,9999
			LUM17	0,0299	0,0166	0,9099
			LUM18	0,0150	0,0193	1,0000
			LUM19	0,0180	0,0150	0,9972
			LUM20	-0,0123	0,0183	1,0000
			LUM3	0,0299	0,0236	0,9925
			LUM4	0,0138	0,0157	0,9999
			LUM7	-0,0026	0,0183	1,0000
			LUM9	0,0004	0,0150	1,0000
			VA7E	0,0182	0,0157	0,9983
			VA7F	0,0173	0,0145	0,9968
		LUM9	LP4BA	-0,0194	0,0103	0,8843
			LUM10	-0,0002	0,0142	1,0000
			LUM11	0,0080	0,0083	0,9998
			LUM12	0,0221	0,0101	0,7208
			LUM14	0,0258	0,0107	0,5787
			LUM16	0,0134	0,0121	0,9992
			LUM17	0,0295	0,0130	0,6697
			LUM18	0,0147	0,0163	0,9998
			LUM19	0,0176	0,0108	0,9627
			LUM20	-0,0126	0,0150	1,0000
			LUM3	0,0295	0,0211	0,9779
			LUM4	0,0135	0,0117	0,9985
			LUM7	-0,0030	0,0151	1,0000
			LUM8	-0,0004	0,0150	1,0000
			VA7E	0,0178	0,0118	0,9804
			VA7F	0,0169	0,0100	0,9438
		VA7E	LP4BA	-0,0372	0,0114	0,1342
			LUM10	-0,0180	0,0150	0,9969
			LUM11	-0,0098	0,0097	0,9996
			LUM12	0,0043	0,0112	1,0000
			LUM14	0,0080	0,0118	1,0000
			LUM16	-0,0044	0,0131	1,0000
			LUM17	0,0117	0,0139	1,0000
			LUM18	-0,0031	0,0170	1,0000
			LUM19	-0,0002	0,0119	1,0000
			LUM20	-0,0304	0,0158	0,8654
			LUM3	0,0117	0,0217	1,0000
			LUM4	-0,0043	0,0127	1,0000
			LUM7	-0,0208	0,0159	0,9909
			LUM8	-0,0182	0,0157	0,9983
			LUM9	-0,0178	0,0118	0,9804
			VA7F	-0,0009	0,0112	1,0000
		VA7F	LP4BA	-0,0363	0,0095	0,0489
			LUM10	-0,0171	0,0136	0,9936
			LUM11	-0,0089	0,0074	0,9952
			LUM12	0,0052	0,0093	1,0000
			LUM14	0,0089	0,0100	0,9999
			LUM16	-0,0035	0,0115	1,0000
			LUM17	0,0126	0,0124	0,9996
			LUM18	-0,0022	0,0158	1,0000
			LUM19	0,0007	0,0101	1,0000
			LUM20	-0,0295	0,0145	0,8079
			LUM3	0,0126	0,0208	1,0000
			LUM4	-0,0034	0,0111	1,0000
			LUM7	-0,0199	0,0146	0,9835
			LUM8	-0,0173	0,0145	0,9968
			LUM9	-0,0169	0,0100	0,9438
			VA7E	0,0009	0,0112	1,0000

Table 5. Post hoc of the m2 of *Megacricetodon gersii*. Both for the length and width we carried out Hochberg's GT2.

		Localities	Localities	Mean Difference	Standard error	Significance
LENGTH m2	Hochberg	LP4BA	LUM10	0,0186	0,0200	1,0000
			LUM11	0,0273	0,0111	0,9143
			LUM12	0,0520	0,0123	0,0059
			LUM14	0,0219	0,0132	1,0000
			LUM16	0,0111	0,0127	1,0000
			LUM17	0,0390	0,0179	0,9940
			LUM18	0,0402	0,0200	0,9995
			LUM19	0,0126	0,0129	1,0000
			LUM2	0,0102	0,0200	1,0000
			LUM20	0,0072	0,0126	1,0000
			LUM3	0,0427	0,0179	0,9522
			LUM4	0,0227	0,0155	1,0000
			LUM5	0,0512	0,0215	0,9545
			LUM7	0,0286	0,0200	1,0000
			LUM8	0,0144	0,0155	1,0000
			LUM9	0,0102	0,0165	1,0000
			VA7E	0,0299	0,0140	0,9960
			VA7F	0,0409	0,0188	0,9942
			VR11	0,0669	0,0200	0,1602
		LUM10	LP4BA	-0,0186	0,0200	1,0000
			LUM11	0,0087	0,0189	1,0000
			LUM12	0,0335	0,0196	1,0000
			LUM14	0,0033	0,0202	1,0000
			LUM16	-0,0075	0,0199	1,0000
			LUM17	0,0204	0,0236	1,0000
			LUM18	0,0217	0,0252	1,0000
			LUM19	-0,0059	0,0200	1,0000
			LUM2	-0,0083	0,0252	1,0000
			LUM20	-0,0113	0,0198	1,0000
			LUM3	0,0242	0,0236	1,0000
			LUM4	0,0042	0,0218	1,0000
			LUM5	0,0327	0,0264	1,0000
			LUM7	0,0100	0,0252	1,0000
			LUM8	-0,0042	0,0218	1,0000
			LUM9	-0,0083	0,0225	1,0000
			VA7E	0,0114	0,0207	1,0000
			VA7F	0,0224	0,0243	1,0000
			VR11	0,0483	0,0252	0,9999
		LUM11	LP4BA	-0,0273	0,0111	0,9143
			LUM10	-0,0087	0,0189	1,0000
			LUM12	0,0247	0,0104	0,9538
			LUM14	-0,0054	0,0114	1,0000
			LUM16	-0,0162	0,0109	1,0000
			LUM17	0,0117	0,0167	1,0000
			LUM18	0,0129	0,0189	1,0000
			LUM19	-0,0147	0,0111	1,0000
			LUM2	-0,0171	0,0189	1,0000
			LUM20	-0,0201	0,0108	1,0000
			LUM3	0,0154	0,0167	1,0000
			LUM4	-0,0046	0,0141	1,0000
			LUM5	0,0239	0,0205	1,0000
			LUM7	0,0013	0,0189	1,0000
			LUM8	-0,0129	0,0141	1,0000
			LUM9	-0,0171	0,0152	1,0000
			VA7E	0,0026	0,0123	1,0000
			VA7F	0,0136	0,0177	1,0000
			VR11	0,0396	0,0189	0,9980
		LUM12	LP4BA	-0,0520	0,0123	0,0059
			LUM10	-0,0335	0,0196	1,0000
			LUM11	-0,0247	0,0104	0,9538
			LUM14	-0,0301	0,0126	0,9499
			LUM16	-0,0410	0,0121	0,1457
			LUM17	-0,0130	0,0175	1,0000
			LUM18	-0,0118	0,0196	1,0000
			LUM19	-0,0394	0,0123	0,2404
			LUM2	-0,0418	0,0196	0,9967
			LUM20	-0,0448	0,0120	0,0427
			LUM3	-0,0093	0,0175	1,0000
			LUM4	-0,0293	0,0151	0,9998
			LUM5	-0,0008	0,0212	1,0000
			LUM7	-0,0235	0,0196	1,0000
			LUM8	-0,0376	0,0151	0,8956
			LUM9	-0,0418	0,0161	0,8213
			VA7E	-0,0221	0,0134	1,0000
			VA7F	-0,0111	0,0184	1,0000
			VR11	0,0149	0,0196	1,0000

Length m2 continued

		Localities	Localities	Mean Difference	Standard error	Significance
LENGTH m2	Hochberg	LUM14	LP4BA	-0,0219	0,0132	1,0000
			LUM10	-0,0033	0,0202	1,0000
			LUM11	0,0054	0,0114	1,0000
			LUM12	0,0301	0,0126	0,9499
			LUM16	-0,0108	0,0130	1,0000
			LUM17	0,0171	0,0181	1,0000
			LUM18	0,0183	0,0202	1,0000
			LUM19	-0,0093	0,0132	1,0000
			LUM2	-0,0117	0,0202	1,0000
			LUM20	-0,0147	0,0129	1,0000
			LUM3	0,0208	0,0181	1,0000
			LUM4	0,0008	0,0158	1,0000
			LUM5	0,0293	0,0217	1,0000
			LUM7	0,0067	0,0202	1,0000
			LUM8	-0,0075	0,0158	1,0000
			LUM9	-0,0117	0,0168	1,0000
			VA7E	0,0080	0,0142	1,0000
			VA7F	0,0190	0,0190	1,0000
			VR11	0,0450	0,0202	0,9890
		LUM16	LP4BA	-0,0111	0,0127	1,0000
			LUM10	0,0075	0,0199	1,0000
			LUM11	0,0162	0,0109	1,0000
			LUM12	0,0410	0,0121	0,1457
			LUM14	0,0108	0,0130	1,0000
			LUM17	0,0279	0,0178	1,0000
			LUM18	0,0292	0,0199	1,0000
			LUM19	0,0016	0,0127	1,0000
			LUM2	-0,0008	0,0199	1,0000
			LUM20	-0,0038	0,0125	1,0000
			LUM3	0,0317	0,0178	1,0000
			LUM4	0,0117	0,0154	1,0000
			LUM5	0,0402	0,0215	1,0000
			LUM7	0,0175	0,0199	1,0000
			LUM8	0,0033	0,0154	1,0000
			LUM9	-0,0008	0,0164	1,0000
			VA7E	0,0189	0,0138	1,0000
			VA7F	0,0299	0,0187	1,0000
			VR11	0,0558	0,0199	0,6197
		LUM17	LP4BA	-0,0390	0,0179	0,9940
			LUM10	-0,0204	0,0236	1,0000
			LUM11	-0,0117	0,0167	1,0000
			LUM12	0,0130	0,0175	1,0000
			LUM14	-0,0171	0,0181	1,0000
			LUM16	-0,0279	0,0178	1,0000
			LUM18	0,0012	0,0236	1,0000
			LUM19	-0,0264	0,0179	1,0000
			LUM2	-0,0288	0,0236	1,0000
			LUM20	-0,0318	0,0177	1,0000
			LUM3	0,0037	0,0218	1,0000
			LUM4	-0,0163	0,0199	1,0000
			LUM5	0,0123	0,0249	1,0000
			LUM7	-0,0104	0,0236	1,0000
			LUM8	-0,0246	0,0199	1,0000
			LUM9	-0,0288	0,0207	1,0000
			VA7E	-0,0090	0,0187	1,0000
			VA7F	0,0020	0,0226	1,0000
			VR11	0,0279	0,0236	1,0000
		LUM18	LP4BA	-0,0402	0,0200	0,9995
			LUM10	-0,0217	0,0252	1,0000
			LUM11	-0,0129	0,0189	1,0000
			LUM12	0,0118	0,0196	1,0000
			LUM14	-0,0183	0,0202	1,0000
			LUM16	-0,0292	0,0199	1,0000
			LUM17	-0,0012	0,0236	1,0000
			LUM19	-0,0276	0,0200	1,0000
			LUM2	-0,0300	0,0252	1,0000
			LUM20	-0,0330	0,0198	1,0000
			LUM3	0,0025	0,0236	1,0000
			LUM4	-0,0175	0,0218	1,0000
			LUM5	0,0110	0,0264	1,0000
			LUM7	-0,0117	0,0252	1,0000
			LUM8	-0,0258	0,0218	1,0000
			LUM9	-0,0300	0,0225	1,0000
			VA7E	-0,0103	0,0207	1,0000
			VA7F	0,0007	0,0243	1,0000
			VR11	0,0267	0,0252	1,0000

Length m2 continued

		Localities	Localities	Mean Difference	Standard error	Significance
LENGTH m2	Hochberg	LUM19	LP4BA	-0,0126	0,0129	1,0000
			LUM10	0,0059	0,0200	1,0000
			LUM11	0,0147	0,0111	1,0000
			LUM12	0,0394	0,0123	0,2404
			LUM14	0,0093	0,0132	1,0000
			LUM16	-0,0016	0,0127	1,0000
			LUM17	0,0264	0,0179	1,0000
			LUM18	0,0276	0,0200	1,0000
			LUM2	-0,0024	0,0200	1,0000
			LUM20	-0,0054	0,0126	1,0000
			LUM3	0,0301	0,0179	1,0000
			LUM4	0,0101	0,0155	1,0000
			LUM5	0,0386	0,0215	1,0000
			LUM7	0,0159	0,0200	1,0000
			LUM8	0,0018	0,0155	1,0000
			LUM9	-0,0024	0,0165	1,0000
			VA7E	0,0173	0,0140	1,0000
			VA7F	0,0283	0,0188	1,0000
			VR11	0,0543	0,0200	0,7144
		LUM2	LP4BA	-0,0102	0,0200	1,0000
			LUM10	0,0083	0,0252	1,0000
			LUM11	0,0171	0,0189	1,0000
			LUM12	0,0418	0,0196	0,9967
			LUM14	0,0117	0,0202	1,0000
			LUM16	0,0008	0,0199	1,0000
			LUM17	0,0288	0,0236	1,0000
			LUM18	0,0300	0,0252	1,0000
			LUM19	0,0024	0,0200	1,0000
			LUM20	-0,0030	0,0198	1,0000
			LUM3	0,0325	0,0236	1,0000
			LUM4	0,0125	0,0218	1,0000
			LUM5	0,0410	0,0264	1,0000
			LUM7	0,0183	0,0252	1,0000
			LUM8	0,0042	0,0218	1,0000
			LUM9	0,0000	0,0225	1,0000
			VA7E	0,0197	0,0207	1,0000
			VA7F	0,0307	0,0243	1,0000
			VR11	0,0567	0,0252	0,9861
		LUM20	LP4BA	-0,0072	0,0126	1,0000
			LUM10	0,0113	0,0198	1,0000
			LUM11	0,0201	0,0108	1,0000
			LUM12	0,0448	0,0120	0,0427
			LUM14	0,0147	0,0129	1,0000
			LUM16	0,0038	0,0125	1,0000
			LUM17	0,0318	0,0177	1,0000
			LUM18	0,0330	0,0198	1,0000
			LUM19	0,0054	0,0126	1,0000
			LUM2	0,0030	0,0198	1,0000
			LUM3	0,0355	0,0177	0,9995
			LUM4	0,0155	0,0153	1,0000
			LUM5	0,0440	0,0214	0,9988
			LUM7	0,0213	0,0198	1,0000
			LUM8	0,0072	0,0153	1,0000
			LUM9	0,0030	0,0163	1,0000
			VA7E	0,0227	0,0137	1,0000
			VA7F	0,0337	0,0187	1,0000
			VR11	0,0597	0,0198	0,4067
		LUM3	LP4BA	-0,0427	0,0179	0,9522
			LUM10	-0,0242	0,0236	1,0000
			LUM11	-0,0154	0,0167	1,0000
			LUM12	0,0093	0,0175	1,0000
			LUM14	-0,0208	0,0181	1,0000
			LUM16	-0,0317	0,0178	1,0000
			LUM17	-0,0037	0,0218	1,0000
			LUM18	-0,0025	0,0236	1,0000
			LUM19	-0,0301	0,0179	1,0000
			LUM2	-0,0325	0,0236	1,0000
			LUM20	-0,0355	0,0177	0,9995
			LUM4	-0,0200	0,0199	1,0000
			LUM5	0,0085	0,0249	1,0000
			LUM7	-0,0142	0,0236	1,0000
			LUM8	-0,0283	0,0199	1,0000
			LUM9	-0,0325	0,0207	1,0000
			VA7E	-0,0128	0,0187	1,0000
			VA7F	-0,0018	0,0226	1,0000
			VR11	0,0242	0,0236	1,0000

Length m2 continued

		Localities	Localities	Mean Difference	Standard error	Significance
LENGTH m2	Hochberg	LUM4	LP4BA	-0,0227	0,0155	1,0000
			LUM10	-0,0042	0,0218	1,0000
			LUM11	0,0046	0,0141	1,0000
			LUM12	0,0293	0,0151	0,9998
			LUM14	-0,0008	0,0158	1,0000
			LUM16	-0,0117	0,0154	1,0000
			LUM17	0,0163	0,0199	1,0000
			LUM18	0,0175	0,0218	1,0000
			LUM19	-0,0101	0,0155	1,0000
			LUM2	-0,0125	0,0218	1,0000
			LUM20	-0,0155	0,0153	1,0000
			LUM3	0,0200	0,0199	1,0000
			LUM5	0,0285	0,0232	1,0000
			LUM7	0,0058	0,0218	1,0000
			LUM8	-0,0083	0,0178	1,0000
			LUM9	-0,0125	0,0187	1,0000
			VA7E	0,0072	0,0165	1,0000
			VA7F	0,0182	0,0208	1,0000
			VR11	0,0442	0,0218	0,9993
		LUM5	LP4BA	-0,0512	0,0215	0,9545
			LUM10	-0,0327	0,0264	1,0000
			LUM11	-0,0239	0,0205	1,0000
			LUM12	0,0008	0,0212	1,0000
			LUM14	-0,0293	0,0217	1,0000
			LUM16	-0,0402	0,0215	1,0000
			LUM17	-0,0123	0,0249	1,0000
			LUM18	-0,0110	0,0264	1,0000
			LUM19	-0,0386	0,0215	1,0000
			LUM2	-0,0410	0,0264	1,0000
			LUM20	-0,0440	0,0214	0,9988
			LUM3	-0,0085	0,0249	1,0000
			LUM4	-0,0285	0,0232	1,0000
			LUM7	-0,0227	0,0264	1,0000
			LUM8	-0,0368	0,0232	1,0000
			LUM9	-0,0410	0,0239	1,0000
			VA7E	-0,0213	0,0222	1,0000
			VA7F	-0,0103	0,0256	1,0000
			VR11	0,0157	0,0264	1,0000
		LUM7	LP4BA	-0,0286	0,0200	1,0000
			LUM10	-0,0100	0,0252	1,0000
			LUM11	-0,0013	0,0189	1,0000
			LUM12	0,0235	0,0196	1,0000
			LUM14	-0,0067	0,0202	1,0000
			LUM16	-0,0175	0,0199	1,0000
			LUM17	0,0104	0,0236	1,0000
			LUM18	0,0117	0,0252	1,0000
			LUM19	-0,0159	0,0200	1,0000
			LUM2	-0,0183	0,0252	1,0000
			LUM20	-0,0213	0,0198	1,0000
			LUM3	0,0142	0,0236	1,0000
			LUM4	-0,0058	0,0218	1,0000
			LUM5	0,0227	0,0264	1,0000
			LUM8	-0,0142	0,0218	1,0000
			LUM9	-0,0183	0,0225	1,0000
			VA7E	0,0014	0,0207	1,0000
			VA7F	0,0124	0,0243	1,0000
			VR11	0,0383	0,0252	1,0000
		LUM8	LP4BA	-0,0144	0,0155	1,0000
			LUM10	0,0042	0,0218	1,0000
			LUM11	0,0129	0,0141	1,0000
			LUM12	0,0376	0,0151	0,8956
			LUM14	0,0075	0,0158	1,0000
			LUM16	-0,0033	0,0154	1,0000
			LUM17	0,0246	0,0199	1,0000
			LUM18	0,0258	0,0218	1,0000
			LUM19	-0,0018	0,0155	1,0000
			LUM2	-0,0042	0,0218	1,0000
			LUM20	-0,0072	0,0153	1,0000
			LUM3	0,0283	0,0199	1,0000
			LUM4	0,0083	0,0178	1,0000
			LUM5	0,0368	0,0232	1,0000
			LUM7	0,0142	0,0218	1,0000
			LUM9	-0,0042	0,0187	1,0000
			VA7E	0,0155	0,0165	1,0000
			VA7F	0,0265	0,0208	1,0000
			VR11	0,0525	0,0218	0,9438

Length m2 continued

		Localities	Localities	Mean Difference	Standard error	Significance
LENGTH m2	Hochberg	LUM9	LP4BA	-0,0102	0,0165	1,0000
			LUM10	0,0083	0,0225	1,0000
			LUM11	0,0171	0,0152	1,0000
			LUM12	0,0418	0,0161	0,8213
			LUM14	0,0117	0,0168	1,0000
			LUM16	0,0008	0,0164	1,0000
			LUM17	0,0288	0,0207	1,0000
			LUM18	0,0300	0,0225	1,0000
			LUM19	0,0024	0,0165	1,0000
			LUM2	0,0000	0,0225	1,0000
			LUM20	-0,0030	0,0163	1,0000
			LUM3	0,0325	0,0207	1,0000
			LUM4	0,0125	0,0187	1,0000
			LUM5	0,0410	0,0239	1,0000
			LUM7	0,0183	0,0225	1,0000
			LUM8	0,0042	0,0187	1,0000
			VA7E	0,0197	0,0174	1,0000
			VA7F	0,0307	0,0215	1,0000
			VR11	0,0567	0,0225	0,8852
		VA7E	LP4BA	-0,0299	0,0140	0,9960
			LUM10	-0,0114	0,0207	1,0000
			LUM11	-0,0026	0,0123	1,0000
			LUM12	0,0221	0,0134	1,0000
			LUM14	-0,0080	0,0142	1,0000
			LUM16	-0,0189	0,0138	1,0000
			LUM17	0,0090	0,0187	1,0000
			LUM18	0,0103	0,0207	1,0000
			LUM19	-0,0173	0,0140	1,0000
			LUM2	-0,0197	0,0207	1,0000
			LUM20	-0,0227	0,0137	1,0000
			LUM3	0,0128	0,0187	1,0000
			LUM4	-0,0072	0,0165	1,0000
			LUM5	0,0213	0,0222	1,0000
			LUM7	-0,0014	0,0207	1,0000
			LUM8	-0,0155	0,0165	1,0000
			LUM9	-0,0197	0,0174	1,0000
			VA7F	0,0110	0,0196	1,0000
			VR11	0,0370	0,0207	1,0000
		VA7F	LP4BA	-0,0409	0,0188	0,9942
			LUM10	-0,0224	0,0243	1,0000
			LUM11	-0,0136	0,0177	1,0000
			LUM12	0,0111	0,0184	1,0000
			LUM14	-0,0190	0,0190	1,0000
			LUM16	-0,0299	0,0187	1,0000
			LUM17	-0,0020	0,0226	1,0000
			LUM18	-0,0007	0,0243	1,0000
			LUM19	-0,0283	0,0188	1,0000
			LUM2	-0,0307	0,0243	1,0000
			LUM20	-0,0337	0,0187	1,0000
			LUM3	0,0018	0,0226	1,0000
			LUM4	-0,0182	0,0208	1,0000
			LUM5	0,0103	0,0256	1,0000
			LUM7	-0,0124	0,0243	1,0000
			LUM8	-0,0265	0,0208	1,0000
			LUM9	-0,0307	0,0215	1,0000
			VA7E	-0,0110	0,0196	1,0000
			VR11	0,0260	0,0243	1,0000
		VR11	LP4BA	-0,0669	0,0200	0,1602
			LUM10	-0,0483	0,0252	0,9999
			LUM11	-0,0396	0,0189	0,9980
			LUM12	-0,0149	0,0196	1,0000
			LUM14	-0,0450	0,0202	0,9890
			LUM16	-0,0558	0,0199	0,6197
			LUM17	-0,0279	0,0236	1,0000
			LUM18	-0,0267	0,0252	1,0000
			LUM19	-0,0543	0,0200	0,7144
			LUM2	-0,0567	0,0252	0,9861
			LUM20	-0,0597	0,0198	0,4067
			LUM3	-0,0242	0,0236	1,0000
			LUM4	-0,0442	0,0218	0,9993
			LUM5	-0,0157	0,0264	1,0000
			LUM7	-0,0383	0,0252	1,0000
			LUM8	-0,0525	0,0218	0,9438
			LUM9	-0,0567	0,0225	0,8852
			VA7E	-0,0370	0,0207	1,0000
			VA7F	-0,0260	0,0243	1,0000

Width m2

		Localities	Localities	Mean Difference	Standard error	Significance
WIDTH m2	Hochberg	LP4BA	LUM10	0,0230	0,0205	1,0000
			LUM11	0,0530	0,0113	0,0006
			LUM12	0,0743	0,0126	0,0000
			LUM14	0,0327	0,0134	0,8853
			LUM16	0,0228	0,0130	1,0000
			LUM17	0,0408	0,0176	0,9485
			LUM18	0,0184	0,0220	1,0000
			LUM19	0,0134	0,0131	1,0000
			LUM2	0,0335	0,0193	1,0000
			LUM20	0,0236	0,0134	1,0000
			LUM3	0,0755	0,0164	0,0010
			LUM4	0,0399	0,0152	0,7297
			LUM8	0,0233	0,0156	1,0000
			LUM9	0,0406	0,0152	0,6822
			VA7E	0,0464	0,0139	0,1377
			VA7F	0,0604	0,0170	0,0638
			VR11	0,0680	0,0205	0,1410
		LUM10	LP4BA	-0,0230	0,0205	1,0000
			LUM11	0,0299	0,0192	1,0000
			LUM12	0,0513	0,0199	0,7832
			LUM14	0,0097	0,0205	1,0000
			LUM16	-0,0003	0,0202	1,0000
			LUM17	0,0178	0,0234	1,0000
			LUM18	-0,0047	0,0269	1,0000
			LUM19	-0,0096	0,0203	1,0000
			LUM2	0,0105	0,0247	1,0000
			LUM20	0,0006	0,0205	1,0000
			LUM3	0,0524	0,0226	0,9470
			LUM4	0,0169	0,0217	1,0000
			LUM8	0,0003	0,0220	1,0000
			LUM9	0,0176	0,0217	1,0000
			VA7E	0,0233	0,0208	1,0000
			VA7F	0,0373	0,0230	1,0000
			VR11	0,0450	0,0257	1,0000
		LUM11	LP4BA	-0,0530	0,0113	0,0006
			LUM10	-0,0299	0,0192	1,0000
			LUM12	0,0213	0,0103	0,9954
			LUM14	-0,0202	0,0113	1,0000
			LUM16	-0,0302	0,0108	0,5497
			LUM17	-0,0122	0,0160	1,0000
			LUM18	-0,0346	0,0208	1,0000
			LUM19	-0,0395	0,0109	0,0529
			LUM2	-0,0195	0,0179	1,0000
			LUM20	-0,0293	0,0113	0,7550
			LUM3	0,0225	0,0147	1,0000
			LUM4	-0,0130	0,0134	1,0000
			LUM8	-0,0297	0,0138	0,9882
			LUM9	-0,0123	0,0134	1,0000
			VA7E	-0,0066	0,0119	1,0000
			VA7F	0,0074	0,0153	1,0000
			VR11	0,0151	0,0192	1,0000
		LUM12	LP4BA	-0,0743	0,0126	0,0000
			LUM10	-0,0513	0,0199	0,7832
			LUM11	-0,0213	0,0103	0,9954
			LUM14	-0,0416	0,0126	0,1480
			LUM16	-0,0515	0,0121	0,0045
			LUM17	-0,0335	0,0170	0,9989
			LUM18	-0,0559	0,0215	0,7581
			LUM19	-0,0608	0,0123	0,0002
			LUM2	-0,0408	0,0187	0,9852
			LUM20	-0,0507	0,0126	0,0109
			LUM3	0,0012	0,0158	1,0000
			LUM4	-0,0344	0,0145	0,9239
			LUM8	-0,0510	0,0148	0,0970
			LUM9	-0,0336	0,0145	0,9462
			VA7E	-0,0279	0,0131	0,9913
			VA7F	-0,0139	0,0163	1,0000
			VR11	-0,0063	0,0199	1,0000
		LUM14	LP4BA	-0,0327	0,0134	0,8853
			LUM10	-0,0097	0,0205	1,0000
			LUM11	0,0202	0,0113	1,0000
			LUM12	0,0416	0,0126	0,1480
			LUM16	-0,0100	0,0130	1,0000
			LUM17	0,0081	0,0176	1,0000
			LUM18	-0,0144	0,0220	1,0000
			LUM19	-0,0193	0,0131	1,0000
			LUM2	0,0008	0,0193	1,0000
			LUM20	-0,0091	0,0134	1,0000
			LUM3	0,0427	0,0164	0,7538
			LUM4	0,0072	0,0152	1,0000
			LUM8	-0,0094	0,0156	1,0000
			LUM9	0,0079	0,0152	1,0000
			VA7E	0,0136	0,0139	1,0000
			VA7F	0,0276	0,0170	1,0000
			VR11	0,0353	0,0205	1,0000

Width m2 continued

		Localities	Localities	Mean Difference	Standard error	Significance
WIDTH m2	Hochberg	LUM16	LP4BA	-0,0228	0,0130	1,0000
			LUM10	0,0003	0,0202	1,0000
			LUM11	0,0302	0,0108	0,5497
			LUM12	0,0515	0,0121	0,0045
			LUM14	0,0100	0,0130	1,0000
			LUM17	0,0180	0,0173	1,0000
			LUM18	-0,0044	0,0218	1,0000
			LUM19	-0,0093	0,0127	1,0000
			LUM2	0,0107	0,0190	1,0000
			LUM20	0,0009	0,0130	1,0000
			LUM3	0,0527	0,0161	0,1631
			LUM4	0,0172	0,0148	1,0000
			LUM8	0,0005	0,0152	1,0000
			LUM9	0,0179	0,0148	1,0000
			VA7E	0,0236	0,0135	1,0000
			VA7F	0,0376	0,0166	0,9680
			VR11	0,0453	0,0202	0,9733
		LUM17	LP4BA	-0,0408	0,0176	0,9485
			LUM10	-0,0178	0,0234	1,0000
			LUM11	0,0122	0,0160	1,0000
			LUM12	0,0335	0,0170	0,9989
			LUM14	-0,0081	0,0176	1,0000
			LUM16	-0,0180	0,0173	1,0000
			LUM18	-0,0224	0,0248	1,0000
			LUM19	-0,0274	0,0174	1,0000
			LUM2	-0,0073	0,0224	1,0000
			LUM20	-0,0172	0,0176	1,0000
			LUM3	0,0346	0,0200	1,0000
			LUM4	-0,0009	0,0190	1,0000
			LUM8	-0,0175	0,0193	1,0000
			LUM9	-0,0002	0,0190	1,0000
			VA7E	0,0056	0,0180	1,0000
			VA7F	0,0196	0,0204	1,0000
			VR11	0,0272	0,0234	1,0000
		LUM18	LP4BA	-0,0184	0,0220	1,0000
			LUM10	0,0047	0,0269	1,0000
			LUM11	0,0346	0,0208	1,0000
			LUM12	0,0559	0,0215	0,7581
			LUM14	0,0144	0,0220	1,0000
			LUM16	0,0044	0,0218	1,0000
			LUM17	0,0224	0,0248	1,0000
			LUM19	-0,0049	0,0219	1,0000
			LUM2	0,0151	0,0260	1,0000
			LUM20	0,0053	0,0220	1,0000
			LUM3	0,0571	0,0240	0,9208
			LUM4	0,0216	0,0232	1,0000
			LUM8	0,0049	0,0234	1,0000
			LUM9	0,0223	0,0232	1,0000
			VA7E	0,0280	0,0224	1,0000
			VA7F	0,0420	0,0244	1,0000
			VR11	0,0497	0,0269	0,9999
		LUM19	LP4BA	-0,0134	0,0131	1,0000
			LUM10	0,0096	0,0203	1,0000
			LUM11	0,0395	0,0109	0,0529
			LUM12	0,0608	0,0123	0,0002
			LUM14	0,0193	0,0131	1,0000
			LUM16	0,0093	0,0127	1,0000
			LUM17	0,0274	0,0174	1,0000
			LUM18	0,0049	0,0219	1,0000
			LUM2	0,0201	0,0191	1,0000
			LUM20	0,0102	0,0131	1,0000
			LUM3	0,0620	0,0162	0,0237
			LUM4	0,0265	0,0150	1,0000
			LUM8	0,0098	0,0153	1,0000
			LUM9	0,0272	0,0150	0,9999
			VA7E	0,0329	0,0137	0,9041
			VA7F	0,0469	0,0167	0,5458
			VR11	0,0546	0,0203	0,6662
		LUM2	LP4BA	-0,0335	0,0193	1,0000
			LUM10	-0,0105	0,0247	1,0000
			LUM11	0,0195	0,0179	1,0000
			LUM12	0,0408	0,0187	0,9852
			LUM14	-0,0008	0,0193	1,0000
			LUM16	-0,0107	0,0190	1,0000
			LUM17	0,0073	0,0224	1,0000
			LUM18	-0,0151	0,0260	1,0000
			LUM19	-0,0201	0,0191	1,0000
			LUM20	-0,0099	0,0193	1,0000
			LUM3	0,0419	0,0215	0,9992
			LUM4	0,0064	0,0206	1,0000
			LUM8	-0,0102	0,0209	1,0000
			LUM9	0,0071	0,0206	1,0000
			VA7E	0,0129	0,0197	1,0000
			VA7F	0,0269	0,0219	1,0000
			VR11	0,0345	0,0247	1,0000

Width m2 continued

		Localities	Localities	Mean Difference	Standard error	Significance
WIDTH m2	Hochberg	LUM20	LP4BA	-0,0236	0,0134	1,0000
			LUM10	-0,0006	0,0205	1,0000
			LUM11	0,0293	0,0113	0,7550
			LUM12	0,0507	0,0126	0,0109
			LUM14	0,0091	0,0134	1,0000
			LUM16	-0,0009	0,0130	1,0000
			LUM17	0,0172	0,0176	1,0000
			LUM18	-0,0053	0,0220	1,0000
			LUM19	-0,0102	0,0131	1,0000
			LUM2	0,0099	0,0193	1,0000
			LUM3	0,0518	0,0164	0,2324
			LUM4	0,0163	0,0152	1,0000
			LUM8	-0,0003	0,0156	1,0000
			LUM9	0,0170	0,0152	1,0000
			VA7E	0,0227	0,0139	1,0000
			VA7F	0,0367	0,0170	0,9870
			VR11	0,0444	0,0205	0,9867
		LUM3	LP4BA	-0,0755	0,0164	0,0010
			LUM10	-0,0524	0,0226	0,9470
			LUM11	-0,0225	0,0147	1,0000
			LUM12	-0,0012	0,0158	1,0000
			LUM14	-0,0427	0,0164	0,7538
			LUM16	-0,0527	0,0161	0,1631
			LUM17	-0,0346	0,0200	1,0000
			LUM18	-0,0571	0,0240	0,9208
			LUM19	-0,0620	0,0162	0,0237
			LUM2	-0,0419	0,0215	0,9992
			LUM20	-0,0518	0,0164	0,2324
			LUM4	-0,0355	0,0179	0,9987
			LUM8	-0,0522	0,0182	0,4828
			LUM9	-0,0348	0,0179	0,9993
			VA7E	-0,0291	0,0169	1,0000
			VA7F	-0,0151	0,0194	1,0000
			VR11	-0,0074	0,0226	1,0000
		LUM4	LP4BA	-0,0399	0,0152	0,7297
			LUM10	-0,0169	0,0217	1,0000
			LUM11	0,0130	0,0134	1,0000
			LUM12	0,0344	0,0145	0,9239
			LUM14	-0,0072	0,0152	1,0000
			LUM16	-0,0172	0,0148	1,0000
			LUM17	0,0009	0,0190	1,0000
			LUM18	-0,0216	0,0232	1,0000
			LUM19	-0,0265	0,0150	1,0000
			LUM2	-0,0064	0,0206	1,0000
			LUM20	-0,0163	0,0152	1,0000
			LUM3	0,0355	0,0179	0,9987
			LUM8	-0,0166	0,0171	1,0000
			LUM9	0,0007	0,0168	1,0000
			VA7E	0,0064	0,0157	1,0000
			VA7F	0,0204	0,0184	1,0000
			VR11	0,0281	0,0217	1,0000
		LUM8	LP4BA	-0,0233	0,0156	1,0000
			LUM10	-0,0003	0,0220	1,0000
			LUM11	0,0297	0,0138	0,9882
			LUM12	0,0510	0,0148	0,0970
			LUM14	0,0094	0,0156	1,0000
			LUM16	-0,0005	0,0152	1,0000
			LUM17	0,0175	0,0193	1,0000
			LUM18	-0,0049	0,0234	1,0000
			LUM19	-0,0098	0,0153	1,0000
			LUM2	0,0102	0,0209	1,0000
			LUM20	0,0003	0,0156	1,0000
			LUM3	0,0522	0,0182	0,4828
			LUM4	0,0166	0,0171	1,0000
			LUM9	0,0174	0,0171	1,0000
			VA7E	0,0231	0,0160	1,0000
			VA7F	0,0371	0,0187	0,9988
			VR11	0,0447	0,0220	0,9972
		LUM9	LP4BA	-0,0406	0,0152	0,6822
			LUM10	-0,0176	0,0217	1,0000
			LUM11	0,0123	0,0134	1,0000
			LUM12	0,0336	0,0145	0,9462
			LUM14	-0,0079	0,0152	1,0000
			LUM16	-0,0179	0,0148	1,0000
			LUM17	0,0002	0,0190	1,0000
			LUM18	-0,0223	0,0232	1,0000
			LUM19	-0,0272	0,0150	0,9999
			LUM2	-0,0071	0,0206	1,0000
			LUM20	-0,0170	0,0152	1,0000
			LUM3	0,0348	0,0179	0,9993
			LUM4	-0,0007	0,0168	1,0000
			LUM8	-0,0174	0,0171	1,0000
			VA7E	0,0057	0,0157	1,0000
			VA7F	0,0197	0,0184	1,0000
			VR11	0,0274	0,0217	1,0000

Width m2 continued

		Localities	Localities	Mean Difference	Standard error	Significance
WIDTH m2	Hochberg	VA7E	LP4BA	-0,0464	0,0139	0,1377
			LUM10	-0,0233	0,0208	1,0000
			LUM11	0,0066	0,0119	1,0000
			LUM12	0,0279	0,0131	0,9913
			LUM14	-0,0136	0,0139	1,0000
			LUM16	-0,0236	0,0135	1,0000
			LUM17	-0,0056	0,0180	1,0000
			LUM18	-0,0280	0,0224	1,0000
			LUM19	-0,0329	0,0137	0,9041
			LUM2	-0,0129	0,0197	1,0000
			LUM20	-0,0227	0,0139	1,0000
			LUM3	0,0291	0,0169	1,0000
			LUM4	-0,0064	0,0157	1,0000
			LUM8	-0,0231	0,0160	1,0000
			LUM9	-0,0057	0,0157	1,0000
			VA7F	0,0140	0,0174	1,0000
			VR11	0,0217	0,0208	1,0000
		VA7F	LP4BA	-0,0604	0,0170	0,0638
			LUM10	-0,0373	0,0230	1,0000
			LUM11	-0,0074	0,0153	1,0000
			LUM12	0,0139	0,0163	1,0000
			LUM14	-0,0276	0,0170	1,0000
			LUM16	-0,0376	0,0166	0,9680
			LUM17	-0,0196	0,0204	1,0000
			LUM18	-0,0420	0,0244	1,0000
			LUM19	-0,0469	0,0167	0,5458
			LUM2	-0,0269	0,0219	1,0000
			LUM20	-0,0367	0,0170	0,9870
			LUM3	0,0151	0,0194	1,0000
			LUM4	-0,0204	0,0184	1,0000
			LUM8	-0,0371	0,0187	0,9988
			LUM9	-0,0197	0,0184	1,0000
			VA7E	-0,0140	0,0174	1,0000
			VR11	0,0077	0,0230	1,0000
		VR11	LP4BA	-0,0680	0,0205	0,1410
			LUM10	-0,0450	0,0257	1,0000
			LUM11	-0,0151	0,0192	1,0000
			LUM12	0,0063	0,0199	1,0000
			LUM14	-0,0353	0,0205	1,0000
			LUM16	-0,0453	0,0202	0,9733
			LUM17	-0,0272	0,0234	1,0000
			LUM18	-0,0497	0,0269	0,9999
			LUM19	-0,0546	0,0203	0,6662
			LUM2	-0,0345	0,0247	1,0000
			LUM20	-0,0444	0,0205	0,9867
			LUM3	0,0074	0,0226	1,0000
			LUM4	-0,0281	0,0217	1,0000
			LUM8	-0,0447	0,0220	0,9972
			LUM9	-0,0274	0,0217	1,0000
			VA7E	-0,0217	0,0208	1,0000
			VA7F	-0,0077	0,0230	1,0000

Table 6. Post hoc of the upper first molars of *Megacricetodon gersii*. Both for the length t and width of the M1, we carried out Games-Howell because of the different variances assumed.

		Localities	Localities	Mean Difference	Standard error	Significance
LENGTH M1	Games-Howell	LP4BA	LUM10	0,0377	0,0091	0,0241
			LUM11	0,0302	0,0108	0,3516
			LUM12	0,0801	0,0211	0,0711
			LUM14	0,0388	0,0149	0,4966
			LUM16	0,0512	0,0165	0,2131
			LUM17	0,0582	0,0178	0,2004
			LUM19	0,0420	0,0190	0,7211
			LUM2	0,0524	0,0382	0,9749
			LUM20	0,0657	0,0137	0,0027
			LUM3	0,1100	0,0178	0,0085
			LUM4	0,1000	0,0203	0,0418
			LUM5	0,0457	0,0206	0,7102
			LUM7	0,0314	0,0178	0,9033
			LUM8	0,0457	0,0168	0,4288
			LUM9	0,0697	0,0269	0,5568
			VA7E	0,0713	0,0198	0,0929
			VA7F	0,0521	0,0288	0,9001
		LUM10	LP4BA	-0,0377	0,0091	0,0241
			LUM11	-0,0075	0,0095	1,0000
			LUM12	0,0424	0,0204	0,7983
			LUM14	0,0011	0,0140	1,0000
			LUM16	0,0135	0,0156	1,0000
			LUM17	0,0205	0,0170	0,9967
			LUM19	0,0042	0,0183	1,0000
			LUM2	0,0147	0,0379	1,0000
			LUM20	0,0280	0,0127	0,7340
			LUM3	0,0723	0,0170	0,0990
			LUM4	0,0623	0,0196	0,3149
			LUM5	0,0080	0,0200	1,0000
			LUM7	-0,0063	0,0170	1,0000
			LUM8	0,0080	0,0159	1,0000
			LUM9	0,0320	0,0264	0,9871
			VA7E	0,0336	0,0191	0,9292
			VA7F	0,0144	0,0284	1,0000
		LUM11	LP4BA	-0,0302	0,0108	0,3516
			LUM10	0,0075	0,0095	1,0000
			LUM12	0,0499	0,0212	0,6450
			LUM14	0,0086	0,0152	1,0000
			LUM16	0,0210	0,0167	0,9975
			LUM17	0,0280	0,0180	0,9699
			LUM19	0,0118	0,0192	1,0000
			LUM2	0,0222	0,0383	1,0000
			LUM20	0,0355	0,0140	0,5108
			LUM3	0,0798	0,0180	0,0604
			LUM4	0,0698	0,0205	0,2278
			LUM5	0,0155	0,0208	0,9999
			LUM7	0,0012	0,0180	1,0000
			LUM8	0,0155	0,0170	0,9999
			LUM9	0,0395	0,0270	0,9572
			VA7E	0,0411	0,0199	0,8132
			VA7F	0,0219	0,0290	1,0000
		LUM12	LP4BA	-0,0801	0,0211	0,0711
			LUM10	-0,0424	0,0204	0,7983
			LUM11	-0,0499	0,0212	0,6450
			LUM14	-0,0413	0,0236	0,9364
			LUM16	-0,0289	0,0246	0,9988
			LUM17	-0,0219	0,0255	1,0000
			LUM19	-0,0381	0,0264	0,9861
			LUM2	-0,0277	0,0423	1,0000
			LUM20	-0,0144	0,0228	1,0000
			LUM3	0,0299	0,0255	0,9983
			LUM4	0,0199	0,0273	1,0000
			LUM5	-0,0344	0,0275	0,9952
			LUM7	-0,0487	0,0255	0,8775
			LUM8	-0,0344	0,0248	0,9918
			LUM9	-0,0104	0,0325	1,0000
			VA7E	-0,0088	0,0269	1,0000
			VA7F	-0,0280	0,0341	1,0000
		LUM14	LP4BA	-0,0388	0,0149	0,4966
			LUM10	-0,0011	0,0140	1,0000
			LUM11	-0,0086	0,0152	1,0000
			LUM12	0,0413	0,0236	0,9364
			LUM16	0,0124	0,0196	1,0000
			LUM17	0,0194	0,0207	0,9999
			LUM19	0,0032	0,0218	1,0000
			LUM2	0,0136	0,0397	1,0000
			LUM20	0,0269	0,0173	0,9775
			LUM3	0,0712	0,0207	0,1697
			LUM4	0,0612	0,0229	0,4750
			LUM5	0,0069	0,0232	1,0000
			LUM7	-0,0074	0,0207	1,0000
			LUM8	0,0069	0,0199	1,0000
			LUM9	0,0309	0,0289	0,9972
			VA7E	0,0325	0,0224	0,9883
			VA7F	0,0133	0,0307	1,0000

Length M1 continued

		Localities	Localities	Mean Difference	Standard error	Significance
LENGTH M1	Games-Howell	LUM16	LP4BA	-0,0512	0,0165	0,2131
			LUM10	-0,0135	0,0156	1,0000
			LUM11	-0,0210	0,0167	0,9975
			LUM12	0,0289	0,0246	0,9988
			LUM14	-0,0124	0,0196	1,0000
			LUM17	0,0070	0,0218	1,0000
			LUM19	-0,0092	0,0229	1,0000
			LUM2	0,0012	0,0403	1,0000
			LUM20	0,0145	0,0187	1,0000
			LUM3	0,0588	0,0218	0,4468
			LUM4	0,0488	0,0239	0,8104
			LUM5	-0,0055	0,0242	1,0000
			LUM7	-0,0197	0,0218	0,9999
			LUM8	-0,0055	0,0210	1,0000
			LUM9	0,0185	0,0297	1,0000
			VA7E	0,0201	0,0235	1,0000
			VA7F	0,0009	0,0315	1,0000
		LUM17	LP4BA	-0,0582	0,0178	0,2004
			LUM10	-0,0205	0,0170	0,9967
			LUM11	-0,0280	0,0180	0,9699
			LUM12	0,0219	0,0255	1,0000
			LUM14	-0,0194	0,0207	0,9999
			LUM16	-0,0070	0,0218	1,0000
			LUM19	-0,0163	0,0238	1,0000
			LUM2	-0,0058	0,0408	1,0000
			LUM20	0,0075	0,0198	1,0000
			LUM3	0,0518	0,0228	0,6935
			LUM4	0,0418	0,0248	0,9417
			LUM5	-0,0125	0,0251	1,0000
			LUM7	-0,0268	0,0228	0,9979
			LUM8	-0,0125	0,0221	1,0000
			LUM9	0,0115	0,0304	1,0000
			VA7E	0,0131	0,0244	1,0000
			VA7F	-0,0061	0,0322	1,0000
		LUM19	LP4BA	-0,0420	0,0190	0,7211
			LUM10	-0,0042	0,0183	1,0000
			LUM11	-0,0118	0,0192	1,0000
			LUM12	0,0381	0,0264	0,9861
			LUM14	-0,0032	0,0218	1,0000
			LUM16	0,0092	0,0229	1,0000
			LUM17	0,0163	0,0238	1,0000
			LUM2	0,0104	0,0414	1,0000
			LUM20	0,0238	0,0210	0,9983
			LUM3	0,0680	0,0238	0,3798
			LUM4	0,0580	0,0258	0,6993
			LUM5	0,0038	0,0260	1,0000
			LUM7	-0,0105	0,0238	1,0000
			LUM8	0,0038	0,0231	1,0000
			LUM9	0,0278	0,0312	0,9997
			VA7E	0,0293	0,0253	0,9986
			VA7F	0,0101	0,0329	1,0000
		LUM2	LP4BA	-0,0524	0,0382	0,9749
			LUM10	-0,0147	0,0379	1,0000
			LUM11	-0,0222	0,0383	1,0000
			LUM12	0,0277	0,0423	1,0000
			LUM14	-0,0136	0,0397	1,0000
			LUM16	-0,0012	0,0403	1,0000
			LUM17	0,0058	0,0408	1,0000
			LUM19	-0,0104	0,0414	1,0000
			LUM20	0,0133	0,0392	1,0000
			LUM3	0,0576	0,0408	0,9747
			LUM4	0,0476	0,0420	0,9964
			LUM5	-0,0067	0,0421	1,0000
			LUM7	-0,0210	0,0408	1,0000
			LUM8	-0,0067	0,0404	1,0000
			LUM9	0,0173	0,0455	1,0000
			VA7E	0,0189	0,0417	1,0000
			VA7F	-0,0003	0,0467	1,0000
		LUM20	LP4BA	-0,0657	0,0137	0,0027
			LUM10	-0,0280	0,0127	0,7340
			LUM11	-0,0355	0,0140	0,5108
			LUM12	0,0144	0,0228	1,0000
			LUM14	-0,0269	0,0173	0,9775
			LUM16	-0,0145	0,0187	1,0000
			LUM17	-0,0075	0,0198	1,0000
			LUM19	-0,0238	0,0210	0,9983
			LUM2	-0,0133	0,0392	1,0000
			LUM3	0,0443	0,0198	0,7105
			LUM4	0,0343	0,0221	0,9634
			LUM5	-0,0200	0,0224	0,9997
			LUM7	-0,0343	0,0198	0,9271
			LUM8	-0,0200	0,0189	0,9996
			LUM9	0,0040	0,0283	1,0000
			VA7E	0,0056	0,0216	1,0000
			VA7F	-0,0136	0,0302	1,0000

Length M1 continued

		Localities	Localities	Mean Difference	Standard error	Significance
LENGTH M1	Games-Howell	LUM3	LP4BA	-0,1100	0,0178	0,0085
			LUM10	-0,0723	0,0170	0,0990
			LUM11	-0,0798	0,0180	0,0604
			LUM12	-0,0299	0,0255	0,9983
			LUM14	-0,0712	0,0207	0,1697
			LUM16	-0,0588	0,0218	0,4468
			LUM17	-0,0518	0,0228	0,6935
			LUM19	-0,0680	0,0238	0,3798
			LUM2	-0,0576	0,0408	0,9747
			LUM20	-0,0443	0,0198	0,7105
			LUM4	-0,0100	0,0249	1,0000
			LUM5	-0,0643	0,0251	0,5440
			LUM7	-0,0786	0,0229	0,1800
			LUM8	-0,0643	0,0221	0,3438
			LUM9	-0,0403	0,0305	0,9850
			VA7E	-0,0387	0,0244	0,9682
			VA7F	-0,0579	0,0322	0,9107
		LUM4	LP4BA	-0,1000	0,0203	0,0418
			LUM10	-0,0623	0,0196	0,3149
			LUM11	-0,0698	0,0205	0,2278
			LUM12	-0,0199	0,0273	1,0000
			LUM14	-0,0612	0,0229	0,4750
			LUM16	-0,0488	0,0239	0,8104
			LUM17	-0,0418	0,0248	0,9417
			LUM19	-0,0580	0,0258	0,6993
			LUM2	-0,0476	0,0420	0,9964
			LUM20	-0,0343	0,0221	0,9634
			LUM3	0,0100	0,0249	1,0000
			LUM5	-0,0543	0,0270	0,8121
			LUM7	-0,0686	0,0249	0,4316
			LUM8	-0,0543	0,0241	0,7015
			LUM9	-0,0303	0,0320	0,9995
			VA7E	-0,0287	0,0263	0,9991
			VA7F	-0,0479	0,0337	0,9857
		LUM5	LP4BA	-0,0457	0,0206	0,7102
			LUM10	-0,0080	0,0200	1,0000
			LUM11	-0,0155	0,0208	0,9999
			LUM12	0,0344	0,0275	0,9952
			LUM14	-0,0069	0,0232	1,0000
			LUM16	0,0055	0,0242	1,0000
			LUM17	0,0125	0,0251	1,0000
			LUM19	-0,0038	0,0260	1,0000
			LUM2	0,0067	0,0421	1,0000
			LUM20	0,0200	0,0224	0,9997
			LUM3	0,0643	0,0251	0,5440
			LUM4	0,0543	0,0270	0,8121
			LUM7	-0,0143	0,0251	1,0000
			LUM8	0,0000	0,0244	1,0000
			LUM9	0,0240	0,0322	1,0000
			VA7E	0,0256	0,0266	0,9997
			VA7F	0,0064	0,0339	1,0000
		LUM7	LP4BA	-0,0314	0,0178	0,9033
			LUM10	0,0063	0,0170	1,0000
			LUM11	-0,0012	0,0180	1,0000
			LUM12	0,0487	0,0255	0,8775
			LUM14	0,0074	0,0207	1,0000
			LUM16	0,0197	0,0218	0,9999
			LUM17	0,0268	0,0228	0,9979
			LUM19	0,0105	0,0238	1,0000
			LUM2	0,0210	0,0408	1,0000
			LUM20	0,0343	0,0198	0,9271
			LUM3	0,0786	0,0229	0,1800
			LUM4	0,0686	0,0249	0,4316
			LUM5	0,0143	0,0251	1,0000
			LUM8	0,0143	0,0221	1,0000
			LUM9	0,0383	0,0305	0,9901
			VA7E	0,0398	0,0244	0,9600
			VA7F	0,0206	0,0322	1,0000
		LUM8	LP4BA	-0,0457	0,0168	0,4288
			LUM10	-0,0080	0,0159	1,0000
			LUM11	-0,0155	0,0170	0,9999
			LUM12	0,0344	0,0248	0,9918
			LUM14	-0,0069	0,0199	1,0000
			LUM16	0,0055	0,0210	1,0000
			LUM17	0,0125	0,0221	1,0000
			LUM19	-0,0038	0,0231	1,0000
			LUM2	0,0067	0,0404	1,0000
			LUM20	0,0200	0,0189	0,9996
			LUM3	0,0643	0,0221	0,3438
			LUM4	0,0543	0,0241	0,7015
			LUM5	0,0000	0,0244	1,0000
			LUM7	-0,0143	0,0221	1,0000
			LUM9	0,0240	0,0299	0,9999
			VA7E	0,0256	0,0237	0,9995
			VA7F	0,0064	0,0317	1,0000

Length M1 continued

		Localities	Localities	[ean Differenc	tandard erro:	Significance
LENGTH M1	Games-Howell	LUM9	LP4BA	-0,0697	0,0269	0,5568
			LUM10	-0,0320	0,0264	0,9871
			LUM11	-0,0395	0,0270	0,9572
			LUM12	0,0104	0,0325	1,0000
			LUM14	-0,0309	0,0289	0,9972
			LUM16	-0,0185	0,0297	1,0000
			LUM17	-0,0115	0,0304	1,0000
			LUM19	-0,0278	0,0312	0,9997
			LUM2	-0,0173	0,0455	1,0000
			LUM20	-0,0040	0,0283	1,0000
			LUM3	0,0403	0,0305	0,9850
			LUM4	0,0303	0,0320	0,9995
			LUM5	-0,0240	0,0322	1,0000
			LUM7	-0,0383	0,0305	0,9901
			LUM8	-0,0240	0,0299	0,9999
			VA7E	0,0016	0,0316	1,0000
			VA7F	-0,0176	0,0380	1,0000
		VA7E	LP4BA	-0,0713	0,0198	0,0929
			LUM10	-0,0336	0,0191	0,9292
			LUM11	-0,0411	0,0199	0,8132
			LUM12	0,0088	0,0269	1,0000
			LUM14	-0,0325	0,0224	0,9883
			LUM16	-0,0201	0,0235	1,0000
			LUM17	-0,0131	0,0244	1,0000
			LUM19	-0,0293	0,0253	0,9986
			LUM2	-0,0189	0,0417	1,0000
			LUM20	-0,0056	0,0216	1,0000
			LUM3	0,0387	0,0244	0,9682
			LUM4	0,0287	0,0263	0,9991
			LUM5	-0,0256	0,0266	0,9997
			LUM7	-0,0398	0,0244	0,9600
			LUM8	-0,0256	0,0237	0,9995
			LUM9	-0,0016	0,0316	1,0000
			VA7F	-0,0192	0,0334	1,0000
		VA7F	LP4BA	-0,0521	0,0288	0,9001
			LUM10	-0,0144	0,0284	1,0000
			LUM11	-0,0219	0,0290	1,0000
			LUM12	0,0280	0,0341	1,0000
			LUM14	-0,0133	0,0307	1,0000
			LUM16	-0,0009	0,0315	1,0000
			LUM17	0,0061	0,0322	1,0000
			LUM19	-0,0101	0,0329	1,0000
			LUM2	0,0003	0,0467	1,0000
			LUM20	0,0136	0,0302	1,0000
			LUM3	0,0579	0,0322	0,9107
			LUM4	0,0479	0,0337	0,9857
			LUM5	-0,0064	0,0339	1,0000
			LUM7	-0,0206	0,0322	1,0000
			LUM8	-0,0064	0,0317	1,0000
			LUM9	0,0176	0,0380	1,0000
			VA7E	0,0192	0,0334	1,0000

Width M1

WIDTH M1

Games-Howell

Localities	Localities	Mean Difference	Standard error	Significance
LP4BA	LUM10	0,0313	0,0125	0,5543
	LUM11	0,0578	0,0077	0,0000
	LUM12	0,0758	0,0100	0,0000
	LUM14	0,0482	0,0108	0,0116
	LUM16	0,0627	0,0089	0,0000
	LUM17	0,0832	0,0110	0,0000
	LUM19	0,0355	0,0122	0,3264
	LUM2	0,0663	0,0186	0,2305
	LUM20	0,0460	0,0103	0,0049
	LUM3	0,0772	0,0187	0,0647
	LUM4	0,0525	0,0091	0,0004
	LUM5	0,0143	0,0234	1,0000
	LUM7	0,0499	0,0140	0,1322
	LUM8	0,0449	0,0115	0,0510
	LUM9	0,0343	0,0112	0,3537
	VA7E	0,0558	0,0138	0,0306
	VA7F	0,0670	0,0129	0,0041
LUM10	LP4BA	-0,0313	0,0125	0,5543
	LUM11	0,0265	0,0122	0,7491
	LUM12	0,0445	0,0138	0,2016
	LUM14	0,0169	0,0144	0,9983
	LUM16	0,0314	0,0130	0,6075
	LUM17	0,0519	0,0145	0,1086
	LUM19	0,0042	0,0155	1,0000
	LUM2	0,0350	0,0209	0,9307
	LUM20	0,0147	0,0140	0,9996
	LUM3	0,0459	0,0210	0,7378
	LUM4	0,0212	0,0131	0,9597
	LUM5	-0,0170	0,0252	1,0000
	LUM7	0,0186	0,0169	0,9991
	LUM8	0,0136	0,0149	0,9999
	LUM9	0,0030	0,0147	1,0000
	VA7E	0,0245	0,0167	0,9862
	VA7F	0,0357	0,0160	0,7171
LUM11	LP4BA	-0,0578	0,0077	0,0000
	LUM10	-0,0265	0,0122	0,7491
	LUM12	0,0180	0,0097	0,9081
	LUM14	-0,0096	0,0105	0,9999
	LUM16	0,0050	0,0086	1,0000
	LUM17	0,0255	0,0107	0,6290
	LUM19	-0,0222	0,0120	0,8948
	LUM2	0,0085	0,0185	1,0000
	LUM20	-0,0118	0,0100	0,9991
	LUM3	0,0195	0,0186	0,9991
	LUM4	-0,0053	0,0087	1,0000
	LUM5	-0,0435	0,0233	0,8439
	LUM7	-0,0078	0,0138	1,0000
	LUM8	-0,0129	0,0112	0,9987
	LUM9	-0,0235	0,0110	0,7504
	VA7E	-0,0020	0,0136	1,0000
	VA7F	0,0093	0,0127	1,0000
LUM12	LP4BA	-0,0758	0,0100	0,0000
	LUM10	-0,0445	0,0138	0,2016
	LUM11	-0,0180	0,0097	0,9081
	LUM14	-0,0276	0,0123	0,7092
	LUM16	-0,0130	0,0107	0,9984
	LUM17	0,0074	0,0124	1,0000
	LUM19	-0,0402	0,0135	0,2833
	LUM2	-0,0095	0,0195	1,0000
	LUM20	-0,0298	0,0118	0,5271
	LUM3	0,0014	0,0196	1,0000
	LUM4	-0,0233	0,0108	0,7616
	LUM5	-0,0615	0,0241	0,5706
	LUM7	-0,0258	0,0151	0,9417
	LUM8	-0,0309	0,0129	0,6125
	LUM9	-0,0415	0,0127	0,2401
	VA7E	-0,0200	0,0150	0,9951
	VA7F	-0,0088	0,0142	1,0000

Width M1 continued

		Localities	Localities	Mean Difference	Standard error	Significance
WIDTH M1	Games-Howell	LUM14	LP4BA	-0,0482	0,0108	0,0116
			LUM10	-0,0169	0,0144	0,9983
			LUM11	0,0096	0,0105	0,9999
			LUM12	0,0276	0,0123	0,7092
			LUM16	0,0146	0,0114	0,9970
			LUM17	0,0350	0,0131	0,4375
			LUM19	-0,0126	0,0141	1,0000
			LUM2	0,0181	0,0199	0,9997
			LUM20	-0,0022	0,0125	1,0000
			LUM3	0,0290	0,0200	0,9828
			LUM4	0,0043	0,0115	1,0000
			LUM5	-0,0339	0,0244	0,9728
			LUM7	0,0018	0,0157	1,0000
			LUM8	-0,0033	0,0135	1,0000
			LUM9	-0,0139	0,0133	0,9992
			VA7E	0,0076	0,0155	1,0000
			VA7F	0,0188	0,0147	0,9965
		LUM16	LP4BA	-0,0627	0,0089	0,0000
			LUM10	-0,0314	0,0130	0,6075
			LUM11	-0,0050	0,0086	1,0000
			LUM12	0,0130	0,0107	0,9984
			LUM14	-0,0146	0,0114	0,9970
			LUM17	0,0205	0,0116	0,9313
			LUM19	-0,0272	0,0128	0,7732
			LUM2	0,0036	0,0190	1,0000
			LUM20	-0,0168	0,0109	0,9838
			LUM3	0,0145	0,0191	1,0000
			LUM4	-0,0103	0,0098	0,9997
			LUM5	-0,0484	0,0237	0,7797
			LUM7	-0,0128	0,0145	0,9999
			LUM8	-0,0179	0,0121	0,9845
			LUM9	-0,0284	0,0119	0,6243
			VA7E	-0,0069	0,0143	1,0000
			VA7F	0,0043	0,0134	1,0000
		LUM17	LP4BA	-0,0832	0,0110	0,0000
			LUM10	-0,0519	0,0145	0,1086
			LUM11	-0,0255	0,0107	0,6290
			LUM12	-0,0074	0,0124	1,0000
			LUM14	-0,0350	0,0131	0,4375
			LUM16	-0,0205	0,0116	0,9313
			LUM19	-0,0477	0,0143	0,1508
			LUM2	-0,0169	0,0200	0,9999
			LUM20	-0,0373	0,0127	0,2865
			LUM3	-0,0060	0,0201	1,0000
			LUM4	-0,0308	0,0117	0,4734
			LUM5	-0,0689	0,0245	0,4654
			LUM7	-0,0333	0,0158	0,7854
			LUM8	-0,0384	0,0137	0,3655
			LUM9	-0,0489	0,0135	0,1403
			VA7E	-0,0274	0,0156	0,9387
			VA7F	-0,0162	0,0149	0,9994
		LUM19	LP4BA	-0,0355	0,0122	0,3264
			LUM10	-0,0042	0,0155	1,0000
			LUM11	0,0222	0,0120	0,8948
			LUM12	0,0402	0,0135	0,2833
			LUM14	0,0126	0,0141	1,0000
			LUM16	0,0272	0,0128	0,7732
			LUM17	0,0477	0,0143	0,1508
			LUM2	0,0308	0,0207	0,9698
			LUM20	0,0104	0,0137	1,0000
			LUM3	0,0417	0,0208	0,8331
			LUM4	0,0169	0,0129	0,9945
			LUM5	-0,0212	0,0251	0,9997
			LUM7	0,0144	0,0167	1,0000
			LUM8	0,0093	0,0147	1,0000
			LUM9	-0,0012	0,0145	1,0000
			VA7E	0,0203	0,0165	0,9980
			VA7F	0,0315	0,0158	0,8466

Width M1 continued

		Localities	Localities	Mean Difference	Standard error	Significance
WIDTH M1	Games-Howell	LUM2	LP4BA	-0,0663	0,0186	0,2305
			LUM10	-0,0350	0,0209	0,9307
			LUM11	-0,0085	0,0185	1,0000
			LUM12	0,0095	0,0195	1,0000
			LUM14	-0,0181	0,0199	0,9997
			LUM16	-0,0036	0,0190	1,0000
			LUM17	0,0169	0,0200	0,9999
			LUM19	-0,0308	0,0207	0,9698
			LUM20	-0,0203	0,0196	0,9986
			LUM3	0,0109	0,0251	1,0000
			LUM4	-0,0138	0,0190	1,0000
			LUM5	-0,0520	0,0288	0,8870
			LUM7	-0,0164	0,0218	1,0000
			LUM8	-0,0214	0,0203	0,9985
			LUM9	-0,0320	0,0202	0,9473
			VA7E	-0,0105	0,0217	1,0000
			VA7F	0,0007	0,0211	1,0000
		LUM20	LP4BA	-0,0460	0,0103	0,0049
			LUM10	-0,0147	0,0140	0,9996
			LUM11	0,0118	0,0100	0,9991
			LUM12	0,0298	0,0118	0,5271
			LUM14	0,0022	0,0125	1,0000
			LUM16	0,0168	0,0109	0,9838
			LUM17	0,0373	0,0127	0,2865
			LUM19	-0,0104	0,0137	1,0000
			LUM2	0,0203	0,0196	0,9986
			LUM3	0,0312	0,0197	0,9641
			LUM4	0,0065	0,0111	1,0000
			LUM5	-0,0317	0,0242	0,9816
			LUM7	0,0040	0,0153	1,0000
			LUM8	-0,0011	0,0131	1,0000
			LUM9	-0,0117	0,0129	0,9998
			VA7E	0,0098	0,0151	1,0000
			VA7F	0,0210	0,0144	0,9865
		LUM3	LP4BA	-0,0772	0,0187	0,0647
			LUM10	-0,0459	0,0210	0,7378
			LUM11	-0,0195	0,0186	0,9991
			LUM12	-0,0014	0,0196	1,0000
			LUM14	-0,0290	0,0200	0,9828
			LUM16	-0,0145	0,0191	1,0000
			LUM17	0,0060	0,0201	1,0000
			LUM19	-0,0417	0,0208	0,8331
			LUM2	-0,0109	0,0251	1,0000
			LUM20	-0,0312	0,0197	0,9641
			LUM4	-0,0248	0,0191	0,9932
			LUM5	-0,0629	0,0288	0,7321
			LUM7	-0,0273	0,0219	0,9965
			LUM8	-0,0323	0,0204	0,9648
			LUM9	-0,0429	0,0203	0,7730
			VA7E	-0,0214	0,0218	0,9998
			VA7F	-0,0102	0,0212	1,0000
		LUM4	LP4BA	-0,0525	0,0091	0,0004
			LUM10	-0,0212	0,0131	0,9597
			LUM11	0,0053	0,0087	1,0000
			LUM12	0,0233	0,0108	0,7616
			LUM14	-0,0043	0,0115	1,0000
			LUM16	0,0103	0,0098	0,9997
			LUM17	0,0308	0,0117	0,4734
			LUM19	-0,0169	0,0129	0,9945
			LUM2	0,0138	0,0190	1,0000
			LUM20	-0,0065	0,0111	1,0000
			LUM3	0,0248	0,0191	0,9932
			LUM5	-0,0382	0,0237	0,9264
			LUM7	-0,0025	0,0146	1,0000
			LUM8	-0,0076	0,0122	1,0000
			LUM9	-0,0182	0,0120	0,9639
			VA7E	0,0033	0,0144	1,0000
			VA7F	0,0146	0,0135	0,9994

Width M1 continued

		Localities	Localities	Mean Difference	Standard error	Significance
WIDTH M1	Games-Howell	LUM5	LP4BA	-0,0143	0,0234	1,0000
			LUM10	0,0170	0,0252	1,0000
			LUM11	0,0435	0,0233	0,8439
			LUM12	0,0615	0,0241	0,5706
			LUM14	0,0339	0,0244	0,9728
			LUM16	0,0484	0,0237	0,7797
			LUM17	0,0689	0,0245	0,4654
			LUM19	0,0212	0,0251	0,9997
			LUM2	0,0520	0,0288	0,8870
			LUM20	0,0317	0,0242	0,9816
			LUM3	0,0629	0,0288	0,7321
			LUM4	0,0382	0,0237	0,9264
			LUM7	0,0356	0,0260	0,9793
			LUM8	0,0306	0,0248	0,9891
			LUM9	0,0200	0,0247	0,9998
			VA7E	0,0415	0,0259	0,9394
			VA7F	0,0527	0,0254	0,7752
		LUM7	LP4BA	-0,0499	0,0140	0,1322
			LUM10	-0,0186	0,0169	0,9991
			LUM11	0,0078	0,0138	1,0000
			LUM12	0,0258	0,0151	0,9417
			LUM14	-0,0018	0,0157	1,0000
			LUM16	0,0128	0,0145	0,9999
			LUM17	0,0333	0,0158	0,7854
			LUM19	-0,0144	0,0167	1,0000
			LUM2	0,0164	0,0218	1,0000
			LUM20	-0,0040	0,0153	1,0000
			LUM3	0,0273	0,0219	0,9965
			LUM4	0,0025	0,0146	1,0000
			LUM5	-0,0356	0,0260	0,9793
			LUM8	-0,0051	0,0162	1,0000
			LUM9	-0,0156	0,0160	0,9997
			VA7E	0,0059	0,0179	1,0000
			VA7F	0,0171	0,0172	0,9998
		LUM8	LP4BA	-0,0449	0,0115	0,0510
			LUM10	-0,0136	0,0149	0,9999
			LUM11	0,0129	0,0112	0,9987
			LUM12	0,0309	0,0129	0,6125
			LUM14	0,0033	0,0135	1,0000
			LUM16	0,0179	0,0121	0,9845
			LUM17	0,0384	0,0137	0,3655
			LUM19	-0,0093	0,0147	1,0000
			LUM2	0,0214	0,0203	0,9985
			LUM20	0,0011	0,0131	1,0000
			LUM3	0,0323	0,0204	0,9648
			LUM4	0,0076	0,0122	1,0000
			LUM5	-0,0306	0,0248	0,9891
			LUM7	0,0051	0,0162	1,0000
			LUM9	-0,0106	0,0139	1,0000
			VA7E	0,0109	0,0160	1,0000
			VA7F	0,0221	0,0152	0,9871
		LUM9	LP4BA	-0,0343	0,0112	0,3537
			LUM10	-0,0030	0,0147	1,0000
			LUM11	0,0235	0,0110	0,7504
			LUM12	0,0415	0,0127	0,2401
			LUM14	0,0139	0,0133	0,9992
			LUM16	0,0284	0,0119	0,6243
			LUM17	0,0489	0,0135	0,1403
			LUM19	0,0012	0,0145	1,0000
			LUM2	0,0320	0,0202	0,9473
			LUM20	0,0117	0,0129	0,9998
			LUM3	0,0429	0,0203	0,7730
			LUM4	0,0182	0,0120	0,9639
			LUM5	-0,0200	0,0247	0,9998
			LUM7	0,0156	0,0160	0,9997
			LUM8	0,0106	0,0139	1,0000
			VA7E	0,0215	0,0158	0,9916
			VA7F	0,0327	0,0151	0,7463

Width M1 continued

		Localities	Localities	Mean Difference	Standard error	Significance
WIDTH M1	Games-Howell	VA7E	LP4BA	-0,0558	0,0138	0,0306
			LUM10	-0,0245	0,0167	0,9862
			LUM11	0,0020	0,0136	1,0000
			LUM12	0,0200	0,0150	0,9951
			LUM14	-0,0076	0,0155	1,0000
			LUM16	0,0069	0,0143	1,0000
			LUM17	0,0274	0,0156	0,9387
			LUM19	-0,0203	0,0165	0,9980
			LUM2	0,0105	0,0217	1,0000
			LUM20	-0,0098	0,0151	1,0000
			LUM3	0,0214	0,0218	0,9998
			LUM4	-0,0033	0,0144	1,0000
			LUM5	-0,0415	0,0259	0,9394
			LUM7	-0,0059	0,0179	1,0000
			LUM8	-0,0109	0,0160	1,0000
			LUM9	-0,0215	0,0158	0,9916
			VA7F	0,0112	0,0170	1,0000
		VA7F	LP4BA	-0,0670	0,0129	0,0041
			LUM10	-0,0357	0,0160	0,7171
			LUM11	-0,0093	0,0127	1,0000
			LUM12	0,0088	0,0142	1,0000
			LUM14	-0,0188	0,0147	0,9965
			LUM16	-0,0043	0,0134	1,0000
			LUM17	0,0162	0,0149	0,9994
			LUM19	-0,0315	0,0158	0,8466
			LUM2	-0,0007	0,0211	1,0000
			LUM20	-0,0210	0,0144	0,9865
			LUM3	0,0102	0,0212	1,0000
			LUM4	-0,0146	0,0135	0,9994
			LUM5	-0,0527	0,0254	0,7752
			LUM7	-0,0171	0,0172	0,9998
			LUM8	-0,0221	0,0152	0,9871
			LUM9	-0,0327	0,0151	0,7463
			VA7E	-0,0112	0,0170	1,0000

Table 7. Post hoc of the M2 of *Megacricetodon gersii*. For the length, we carried out Games-Howell; and for the width we carried out Hochberg's GT2.

		Localities	Localities	Mean Difference	Standard error	Significance
LENGTH M2	Games-Howell	LP4BA	LUM10	0,0088	0,0242	1,0000
			LUM11	0,0215	0,0110	0,8846
			LUM12	0,0354	0,0132	0,4499
			LUM14	0,0438	0,0127	0,1088
			LUM16	0,0158	0,0123	0,9981
			LUM17	0,0368	0,0220	0,9512
			LUM18	0,0221	0,0250	0,9998
			LUM19	-0,0026	0,0174	1,0000
			LUM20	-0,0199	0,0138	0,9926
			LUM3	0,0664	0,0137	0,0032
			LUM4	0,0254	0,0192	0,9952
			LUM7	0,0514	0,0185	0,4075
			LUM8	0,0237	0,0155	0,9828
			LUM9	0,0152	0,0235	1,0000
			VA7D	0,0277	0,0205	0,9924
			VA7E	0,0188	0,0150	0,9983
			VA7F	0,0600	0,0334	0,9025
			VR11	0,0138	0,0298	1,0000
		LUM10	LP4BA	-0,0088	0,0242	1,0000
			LUM11	0,0127	0,0227	1,0000
			LUM12	0,0267	0,0239	0,9939
			LUM14	0,0350	0,0236	0,9519
			LUM16	0,0071	0,0234	1,0000
			LUM17	0,0280	0,0296	0,9996
			LUM18	0,0133	0,0320	1,0000
			LUM19	-0,0114	0,0264	1,0000
			LUM20	-0,0287	0,0242	0,9908
			LUM3	0,0577	0,0242	0,6569
			LUM4	0,0167	0,0276	1,0000
			LUM7	0,0427	0,0272	0,9512
			LUM8	0,0150	0,0252	1,0000
			LUM9	0,0064	0,0308	1,0000
			VA7D	0,0190	0,0285	1,0000
			VA7E	0,0100	0,0249	1,0000
			VA7F	0,0513	0,0388	0,9915
			VR11	0,0050	0,0358	1,0000

Length M2 continued

		Localities	Localities	Mean Difference	Standard error	Significance
LENGTH M2	Games-Howell	LUM11	LP4BA	-0,0215	0,0110	0,8846
			LUM10	-0,0127	0,0227	1,0000
			LUM12	0,0139	0,0102	0,9949
			LUM14	0,0223	0,0095	0,6712
			LUM16	-0,0056	0,0090	1,0000
			LUM17	0,0153	0,0203	1,0000
			LUM18	0,0006	0,0235	1,0000
			LUM19	-0,0241	0,0152	0,9656
			LUM20	-0,0414	0,0109	0,0590
			LUM3	0,0449	0,0108	0,0338
			LUM4	0,0039	0,0172	1,0000
			LUM7	0,0300	0,0165	0,9131
			LUM8	0,0023	0,0130	1,0000
			LUM9	-0,0063	0,0219	1,0000
			VA7D	0,0063	0,0186	1,0000
			VA7E	-0,0027	0,0124	1,0000
			VA7F	0,0385	0,0323	0,9953
			VR11	-0,0077	0,0286	1,0000
		LUM12	LP4BA	-0,0354	0,0132	0,4499
			LUM10	-0,0267	0,0239	0,9939
			LUM11	-0,0139	0,0102	0,9949
			LUM14	0,0083	0,0120	1,0000
			LUM16	-0,0196	0,0116	0,9648
			LUM17	0,0013	0,0216	1,0000
			LUM18	-0,0133	0,0247	1,0000
			LUM19	-0,0380	0,0169	0,7231
			LUM20	-0,0554	0,0132	0,0182
			LUM3	0,0310	0,0131	0,6597
			LUM4	-0,0100	0,0188	1,0000
			LUM7	0,0160	0,0180	1,0000
			LUM8	-0,0117	0,0149	1,0000
			LUM9	-0,0202	0,0231	0,9999
			VA7D	-0,0077	0,0200	1,0000
			VA7E	-0,0167	0,0144	0,9993
			VA7F	0,0246	0,0331	1,0000
			VR11	-0,0217	0,0295	1,0000
		LUM14	LP4BA	-0,0438	0,0127	0,1088
			LUM10	-0,0350	0,0236	0,9519
			LUM11	-0,0223	0,0095	0,6712
			LUM12	-0,0083	0,0120	1,0000
			LUM16	-0,0279	0,0110	0,5478
			LUM17	-0,0070	0,0213	1,0000
			LUM18	-0,0217	0,0244	0,9997
			LUM19	-0,0464	0,0165	0,4042
			LUM20	-0,0637	0,0127	0,0021
			LUM3	0,0227	0,0126	0,9347
			LUM4	-0,0183	0,0184	0,9998
			LUM7	0,0077	0,0177	1,0000
			LUM8	-0,0200	0,0145	0,9930
			LUM9	-0,0286	0,0228	0,9931
			VA7D	-0,0160	0,0197	1,0000
			VA7E	-0,0250	0,0140	0,9349
			VA7F	0,0162	0,0329	1,0000
			VR11	-0,0300	0,0293	0,9985
		LUM16	LP4BA	-0,0158	0,0123	0,9981
			LUM10	-0,0071	0,0234	1,0000
			LUM11	0,0056	0,0090	1,0000
			LUM12	0,0196	0,0116	0,9648
			LUM14	0,0279	0,0110	0,5478
			LUM17	0,0209	0,0210	0,9997
			LUM18	0,0062	0,0242	1,0000
			LUM19	-0,0184	0,0162	0,9989
			LUM20	-0,0358	0,0123	0,3122
			LUM3	0,0506	0,0122	0,0244
			LUM4	0,0096	0,0181	1,0000
			LUM7	0,0356	0,0174	0,8291
			LUM8	0,0079	0,0141	1,0000
			LUM9	-0,0007	0,0226	1,0000
			VA7D	0,0119	0,0195	1,0000
			VA7E	0,0029	0,0136	1,0000
			VA7F	0,0442	0,0328	0,9868
			VR11	-0,0021	0,0291	1,0000
		LUM17	LP4BA	-0,0368	0,0220	0,9512
			LUM10	-0,0280	0,0296	0,9996
			LUM11	-0,0153	0,0203	1,0000
			LUM12	-0,0013	0,0216	1,0000
			LUM14	0,0070	0,0213	1,0000
			LUM16	-0,0209	0,0210	0,9997
			LUM18	-0,0147	0,0303	1,0000
			LUM19	-0,0394	0,0243	0,9663
			LUM20	-0,0567	0,0219	0,5353
			LUM3	0,0297	0,0219	0,9918
			LUM4	-0,0113	0,0257	1,0000
			LUM7	0,0147	0,0252	1,0000
			LUM8	-0,0130	0,0230	1,0000
			LUM9	-0,0216	0,0290	1,0000
			VA7D	-0,0090	0,0266	1,0000
			VA7E	-0,0180	0,0227	1,0000
			VA7F	0,0232	0,0375	1,0000
			VR11	-0,0230	0,0344	1,0000

Length M2 continued

		Localities	Localities	Mean Difference	Standard error	Significance
LENGTH M2	Games-Howell	LUM18	LP4BA	-0,0221	0,0250	0,9998
			LUM10	-0,0133	0,0320	1,0000
			LUM11	-0,0006	0,0235	1,0000
			LUM12	0,0133	0,0247	1,0000
			LUM14	0,0217	0,0244	0,9997
			LUM16	-0,0062	0,0242	1,0000
			LUM17	0,0147	0,0303	1,0000
			LUM19	-0,0247	0,0271	0,9998
			LUM20	-0,0420	0,0250	0,9286
			LUM3	0,0443	0,0249	0,9013
			LUM4	0,0033	0,0283	1,0000
			LUM7	0,0294	0,0279	0,9991
			LUM8	0,0017	0,0259	1,0000
			LUM9	-0,0069	0,0314	1,0000
			VA7D	0,0057	0,0292	1,0000
			VA7E	-0,0033	0,0257	1,0000
			VA7F	0,0379	0,0393	0,9998
			VR11	-0,0083	0,0364	1,0000
		LUM19	LP4BA	0,0026	0,0174	1,0000
			LUM10	0,0114	0,0264	1,0000
			LUM11	0,0241	0,0152	0,9656
			LUM12	0,0380	0,0169	0,7231
			LUM14	0,0464	0,0165	0,4042
			LUM16	0,0184	0,0162	0,9989
			LUM17	0,0394	0,0243	0,9663
			LUM18	0,0247	0,0271	0,9998
			LUM20	-0,0173	0,0173	0,9998
			LUM3	0,0690	0,0173	0,0556
			LUM4	0,0280	0,0219	0,9969
			LUM7	0,0541	0,0213	0,5480
			LUM8	0,0264	0,0187	0,9913
			LUM9	0,0178	0,0257	1,0000
			VA7D	0,0304	0,0230	0,9951
			VA7E	0,0214	0,0183	0,9989
			VA7F	0,0626	0,0350	0,9107
			VR11	0,0164	0,0316	1,0000
		LUM20	LP4BA	0,0199	0,0138	0,9926
			LUM10	0,0287	0,0242	0,9908
			LUM11	0,0414	0,0109	0,0590
			LUM12	0,0554	0,0132	0,0182
			LUM14	0,0637	0,0127	0,0021
			LUM16	0,0358	0,0123	0,3122
			LUM17	0,0567	0,0219	0,5353
			LUM18	0,0420	0,0250	0,9286
			LUM19	0,0173	0,0173	0,9998
			LUM3	0,0864	0,0137	0,0001
			LUM4	0,0454	0,0192	0,6569
			LUM7	0,0714	0,0185	0,0633
			LUM8	0,0437	0,0155	0,3770
			LUM9	0,0351	0,0234	0,9719
			VA7D	0,0477	0,0204	0,6751
			VA7E	0,0387	0,0150	0,5172
			VA7F	0,0799	0,0334	0,6426
			VR11	0,0337	0,0298	0,9964
		LUM3	LP4BA	-0,0664	0,0137	0,0032
			LUM10	-0,0577	0,0242	0,6569
			LUM11	-0,0449	0,0108	0,0338
			LUM12	-0,0310	0,0131	0,6597
			LUM14	-0,0227	0,0126	0,9347
			LUM16	-0,0506	0,0122	0,0244
			LUM17	-0,0297	0,0219	0,9918
			LUM18	-0,0443	0,0249	0,9013
			LUM19	-0,0690	0,0173	0,0556
			LUM20	-0,0864	0,0137	0,0001
			LUM4	-0,0410	0,0191	0,7818
			LUM7	-0,0150	0,0184	1,0000
			LUM8	-0,0427	0,0154	0,4098
			LUM9	-0,0512	0,0234	0,7435
			VA7D	-0,0387	0,0204	0,8865
			VA7E	-0,0477	0,0149	0,2027
			VA7F	-0,0064	0,0333	1,0000
			VR11	-0,0527	0,0298	0,9000
		LUM4	LP4BA	-0,0254	0,0192	0,9952
			LUM10	-0,0167	0,0276	1,0000
			LUM11	-0,0039	0,0172	1,0000
			LUM12	0,0100	0,0188	1,0000
			LUM14	0,0183	0,0184	0,9998
			LUM16	-0,0096	0,0181	1,0000
			LUM17	0,0113	0,0257	1,0000
			LUM18	-0,0033	0,0283	1,0000
			LUM19	-0,0280	0,0219	0,9969
			LUM20	-0,0454	0,0192	0,6569
			LUM3	0,0410	0,0191	0,7818
			LUM7	0,0260	0,0228	0,9992
			LUM8	-0,0017	0,0204	1,0000
			LUM9	-0,0102	0,0270	1,0000
			VA7D	0,0023	0,0244	1,0000
			VA7E	-0,0067	0,0200	1,0000
			VA7F	0,0346	0,0359	0,9997
			VR11	-0,0117	0,0326	1,0000

Length M2 continued

		Localities	Localities	Mean Difference	Standard error	Significance
LENGTH M2	Games-Howell	LUM7	LP4BA	-0,0514	0,0185	0,4075
			LUM10	-0,0427	0,0272	0,9512
			LUM11	-0,0300	0,0165	0,9131
			LUM12	-0,0160	0,0180	1,0000
			LUM14	-0,0077	0,0177	1,0000
			LUM16	-0,0356	0,0174	0,8291
			LUM17	-0,0147	0,0252	1,0000
			LUM18	-0,0294	0,0279	0,9991
			LUM19	-0,0541	0,0213	0,5480
			LUM20	-0,0714	0,0185	0,0633
			LUM3	0,0150	0,0184	1,0000
			LUM4	-0,0260	0,0228	0,9992
			LUM8	-0,0277	0,0198	0,9923
			LUM9	-0,0363	0,0265	0,9903
			VA7D	-0,0237	0,0239	0,9998
			VA7E	-0,0327	0,0194	0,9580
			VA7F	0,0086	0,0356	1,0000
			VR11	-0,0377	0,0322	0,9967
		LUM8	LP4BA	-0,0237	0,0155	0,9828
			LUM10	-0,0150	0,0252	1,0000
			LUM11	-0,0023	0,0130	1,0000
			LUM12	0,0117	0,0149	1,0000
			LUM14	0,0200	0,0145	0,9930
			LUM16	-0,0079	0,0141	1,0000
			LUM17	0,0130	0,0230	1,0000
			LUM18	-0,0017	0,0259	1,0000
			LUM19	-0,0264	0,0187	0,9913
			LUM20	-0,0437	0,0155	0,3770
			LUM3	0,0427	0,0154	0,4098
			LUM4	0,0017	0,0204	1,0000
			LUM7	0,0277	0,0198	0,9923
			LUM9	-0,0086	0,0245	1,0000
			VA7D	0,0040	0,0216	1,0000
			VA7E	-0,0050	0,0165	1,0000
			VA7F	0,0363	0,0341	0,9989
			VR11	-0,0100	0,0306	1,0000
		LUM9	LP4BA	-0,0152	0,0235	1,0000
			LUM10	-0,0064	0,0308	1,0000
			LUM11	0,0063	0,0219	1,0000
			LUM12	0,0202	0,0231	0,9999
			LUM14	0,0286	0,0228	0,9931
			LUM16	0,0007	0,0226	1,0000
			LUM17	0,0216	0,0290	1,0000
			LUM18	0,0069	0,0314	1,0000
			LUM19	-0,0178	0,0257	1,0000
			LUM20	-0,0351	0,0234	0,9719
			LUM3	0,0512	0,0234	0,7435
			LUM4	0,0102	0,0270	1,0000
			LUM7	0,0363	0,0265	0,9903
			LUM8	0,0086	0,0245	1,0000
			VA7D	0,0126	0,0279	1,0000
			VA7E	0,0036	0,0242	1,0000
			VA7F	0,0448	0,0384	0,9980
			VR11	-0,0014	0,0353	1,0000
		VA7D	LP4BA	-0,0277	0,0205	0,9924
			LUM10	-0,0190	0,0285	1,0000
			LUM11	-0,0063	0,0186	1,0000
			LUM12	0,0077	0,0200	1,0000
			LUM14	0,0160	0,0197	1,0000
			LUM16	-0,0119	0,0195	1,0000
			LUM17	0,0090	0,0266	1,0000
			LUM18	-0,0057	0,0292	1,0000
			LUM19	-0,0304	0,0230	0,9951
			LUM20	-0,0477	0,0204	0,6751
			LUM3	0,0387	0,0204	0,8865
			LUM4	-0,0023	0,0244	1,0000
			LUM7	0,0237	0,0239	0,9998
			LUM8	-0,0040	0,0216	1,0000
			LUM9	-0,0126	0,0279	1,0000
			VA7E	-0,0090	0,0213	1,0000
			VA7F	0,0323	0,0366	0,9999
			VR11	-0,0140	0,0334	1,0000
		VA7E	LP4BA	-0,0188	0,0150	0,9983
			LUM10	-0,0100	0,0249	1,0000
			LUM11	0,0027	0,0124	1,0000
			LUM12	0,0167	0,0144	0,9993
			LUM14	0,0250	0,0140	0,9349
			LUM16	-0,0029	0,0136	1,0000
			LUM17	0,0180	0,0227	1,0000
			LUM18	0,0033	0,0257	1,0000
			LUM19	-0,0214	0,0183	0,9989
			LUM20	-0,0387	0,0150	0,5172
			LUM3	0,0477	0,0149	0,2027
			LUM4	0,0067	0,0200	1,0000
			LUM7	0,0327	0,0194	0,9580
			LUM8	0,0050	0,0165	1,0000
			LUM9	-0,0036	0,0242	1,0000
			VA7D	0,0090	0,0213	1,0000
			VA7F	0,0413	0,0339	0,9954
			VR11	-0,0050	0,0304	1,0000

Length M2 continued

		Localities	Localities	Mean Difference	Standard error	Significance
LENGTH M2	Games-Howell	VA7F	LP4BA	-0,0600	0,0334	0,9025
			LUM10	-0,0513	0,0388	0,9915
			LUM11	-0,0385	0,0323	0,9953
			LUM12	-0,0246	0,0331	1,0000
			LUM14	-0,0162	0,0329	1,0000
			LUM16	-0,0442	0,0328	0,9868
			LUM17	-0,0232	0,0375	1,0000
			LUM18	-0,0379	0,0393	0,9998
			LUM19	-0,0626	0,0350	0,9107
			LUM20	-0,0799	0,0334	0,6426
			LUM3	0,0064	0,0333	1,0000
			LUM4	-0,0346	0,0359	0,9997
			LUM7	-0,0086	0,0356	1,0000
			LUM8	-0,0363	0,0341	0,9989
			LUM9	-0,0448	0,0384	0,9980
			VA7D	-0,0323	0,0366	0,9999
			VA7E	-0,0413	0,0339	0,9954
			VR11	-0,0462	0,0426	0,9991
		VR11	LP4BA	-0,0138	0,0298	1,0000
			LUM10	-0,0050	0,0358	1,0000
			LUM11	0,0077	0,0286	1,0000
			LUM12	0,0217	0,0295	1,0000
			LUM14	0,0300	0,0293	0,9985
			LUM16	0,0021	0,0291	1,0000
			LUM17	0,0230	0,0344	1,0000
			LUM18	0,0083	0,0364	1,0000
			LUM19	-0,0164	0,0316	1,0000
			LUM20	-0,0337	0,0298	0,9964
			LUM3	0,0527	0,0298	0,9000
			LUM4	0,0117	0,0326	1,0000
			LUM7	0,0377	0,0322	0,9967
			LUM8	0,0100	0,0306	1,0000
			LUM9	0,0014	0,0353	1,0000
			VA7D	0,0140	0,0334	1,0000
			VA7E	0,0050	0,0304	1,0000
			VA7F	0,0462	0,0426	0,9991

Width M2

		Localities	Localities	Mean Difference	Standard error	Significance
WIDTH M2	Hochberg	LP4BA	LUM10	0,0116	0,0196	1,0000
			LUM11	0,0143	0,0099	1,0000
			LUM12	0,0308	0,0125	0,8929
			LUM14	0,0418	0,0133	0,2626
			LUM16	0,0078	0,0109	1,0000
			LUM17	0,0151	0,0144	1,0000
			LUM18	0,0036	0,0196	1,0000
			LUM19	-0,0134	0,0149	1,0000
			LUM20	-0,0186	0,0115	1,0000
			LUM3	0,0465	0,0136	0,1137
			LUM4	0,0129	0,0130	1,0000
			LUM7	0,0139	0,0133	1,0000
			LUM8	-0,0119	0,0136	1,0000
			LUM9	-0,0054	0,0181	1,0000
			VA7D	0,0233	0,0144	1,0000
			VA7E	0,0096	0,0127	1,0000
			VA7F	0,0307	0,0155	0,9993
			VR11	0,0353	0,0170	0,9973
		LUM10	LP4BA	-0,0116	0,0196	1,0000
			LUM11	0,0027	0,0189	1,0000
			LUM12	0,0192	0,0204	1,0000
			LUM14	0,0301	0,0209	1,0000
			LUM16	-0,0038	0,0194	1,0000
			LUM17	0,0035	0,0216	1,0000
			LUM18	-0,0080	0,0253	1,0000
			LUM19	-0,0250	0,0219	1,0000
			LUM20	-0,0303	0,0198	1,0000
			LUM3	0,0349	0,0211	1,0000
			LUM4	0,0013	0,0207	1,0000
			LUM7	0,0023	0,0209	1,0000
			LUM8	-0,0235	0,0211	1,0000
			LUM9	-0,0170	0,0242	1,0000
			VA7D	0,0116	0,0216	1,0000
			VA7E	-0,0020	0,0205	1,0000
			VA7F	0,0191	0,0223	1,0000
			VR11	0,0237	0,0234	1,0000

Width M2 continued

		Localities	Localities	Mean Difference	Standard error	Significance
WIDTH M2	Hochberg	LUM11	LP4BA	-0,0143	0,0099	1,0000
			LUM10	-0,0027	0,0189	1,0000
			LUM12	0,0165	0,0114	1,0000
			LUM14	0,0275	0,0123	0,9806
			LUM16	-0,0065	0,0096	1,0000
			LUM17	0,0008	0,0135	1,0000
			LUM18	-0,0107	0,0189	1,0000
			LUM19	-0,0277	0,0140	0,9994
			LUM20	-0,0329	0,0103	0,2201
			LUM3	0,0323	0,0126	0,8250
			LUM4	-0,0013	0,0119	1,0000
			LUM7	-0,0004	0,0123	1,0000
			LUM8	-0,0262	0,0126	0,9971
			LUM9	-0,0197	0,0174	1,0000
			VA7D	0,0090	0,0135	1,0000
			VA7E	-0,0047	0,0117	1,0000
			VA7F	0,0164	0,0146	1,0000
			VR11	0,0210	0,0163	1,0000
		LUM12	LP4BA	-0,0308	0,0125	0,8929
			LUM10	-0,0192	0,0204	1,0000
			LUM11	-0,0165	0,0114	1,0000
			LUM14	0,0110	0,0145	1,0000
			LUM16	-0,0230	0,0123	0,9999
			LUM17	-0,0157	0,0155	1,0000
			LUM18	-0,0272	0,0204	1,0000
			LUM19	-0,0442	0,0160	0,6203
			LUM20	-0,0494	0,0128	0,0238
			LUM3	0,0157	0,0148	1,0000
			LUM4	-0,0178	0,0142	1,0000
			LUM7	-0,0169	0,0145	1,0000
			LUM8	-0,0427	0,0148	0,4861
			LUM9	-0,0362	0,0190	0,9998
			VA7D	-0,0075	0,0155	1,0000
			VA7E	-0,0212	0,0139	1,0000
			VA7F	-0,0001	0,0165	1,0000
			VR11	0,0045	0,0180	1,0000
		LUM14	LP4BA	-0,0418	0,0133	0,2626
			LUM10	-0,0301	0,0209	1,0000
			LUM11	-0,0275	0,0123	0,9806
			LUM12	-0,0110	0,0145	1,0000
			LUM16	-0,0339	0,0131	0,7992
			LUM17	-0,0267	0,0161	1,0000
			LUM18	-0,0381	0,0209	1,0000
			LUM19	-0,0551	0,0166	0,1543
			LUM20	-0,0604	0,0136	0,0021
			LUM3	0,0048	0,0154	1,0000
			LUM4	-0,0288	0,0149	0,9997
			LUM7	-0,0279	0,0151	1,0000
			LUM8	-0,0537	0,0154	0,0934
			LUM9	-0,0471	0,0195	0,9230
			VA7D	-0,0185	0,0161	1,0000
			VA7E	-0,0321	0,0147	0,9882
			VA7F	-0,0110	0,0171	1,0000
			VR11	-0,0064	0,0185	1,0000
		LUM16	LP4BA	-0,0078	0,0109	1,0000
			LUM10	0,0038	0,0194	1,0000
			LUM11	0,0065	0,0096	1,0000
			LUM12	0,0230	0,0123	0,9999
			LUM14	0,0339	0,0131	0,7992
			LUM17	0,0072	0,0142	1,0000
			LUM18	-0,0042	0,0194	1,0000
			LUM19	-0,0212	0,0148	1,0000
			LUM20	-0,0265	0,0113	0,9510
			LUM3	0,0387	0,0134	0,5016
			LUM4	0,0051	0,0128	1,0000
			LUM7	0,0061	0,0131	1,0000
			LUM8	-0,0198	0,0134	1,0000
			LUM9	-0,0132	0,0180	1,0000
			VA7D	0,0154	0,0142	1,0000
			VA7E	0,0018	0,0125	1,0000
			VA7F	0,0229	0,0153	1,0000
			VR11	0,0275	0,0169	1,0000

Width M2 continued

		Localities	Localities	Mean Difference	Standard error	Significance
WIDTH M2	Hochberg	LUM17	LP4BA	-0,0151	0,0144	1,0000
			LUM10	-0,0035	0,0216	1,0000
			LUM11	-0,0008	0,0135	1,0000
			LUM12	0,0157	0,0155	1,0000
			LUM14	0,0267	0,0161	1,0000
			LUM16	-0,0072	0,0142	1,0000
			LUM18	-0,0115	0,0216	1,0000
			LUM19	-0,0285	0,0175	1,0000
			LUM20	-0,0337	0,0147	0,9680
			LUM3	0,0315	0,0164	0,9998
			LUM4	-0,0021	0,0159	1,0000
			LUM7	-0,0012	0,0161	1,0000
			LUM8	-0,0270	0,0164	1,0000
			LUM9	-0,0205	0,0203	1,0000
			VA7D	0,0082	0,0171	1,0000
			VA7E	-0,0055	0,0157	1,0000
			VA7F	0,0157	0,0180	1,0000
			VR11	0,0203	0,0194	1,0000
		LUM18	LP4BA	-0,0036	0,0196	1,0000
			LUM10	0,0080	0,0253	1,0000
			LUM11	0,0107	0,0189	1,0000
			LUM12	0,0272	0,0204	1,0000
			LUM14	0,0381	0,0209	1,0000
			LUM16	0,0042	0,0194	1,0000
			LUM17	0,0115	0,0216	1,0000
			LUM19	-0,0170	0,0219	1,0000
			LUM20	-0,0223	0,0198	1,0000
			LUM3	0,0429	0,0211	0,9984
			LUM4	0,0093	0,0207	1,0000
			LUM7	0,0103	0,0209	1,0000
			LUM8	-0,0155	0,0211	1,0000
			LUM9	-0,0090	0,0242	1,0000
			VA7D	0,0196	0,0216	1,0000
			VA7E	0,0060	0,0205	1,0000
			VA7F	0,0271	0,0223	1,0000
			VR11	0,0317	0,0234	1,0000
		LUM19	LP4BA	0,0134	0,0149	1,0000
			LUM10	0,0250	0,0219	1,0000
			LUM11	0,0277	0,0140	0,9994
			LUM12	0,0442	0,0160	0,6203
			LUM14	0,0551	0,0166	0,1543
			LUM16	0,0212	0,0148	1,0000
			LUM17	0,0285	0,0175	1,0000
			LUM18	0,0170	0,0219	1,0000
			LUM20	-0,0053	0,0152	1,0000
			LUM3	0,0599	0,0168	0,0718
			LUM4	0,0263	0,0163	1,0000
			LUM7	0,0273	0,0166	1,0000
			LUM8	0,0015	0,0168	1,0000
			LUM9	0,0080	0,0207	1,0000
			VA7D	0,0366	0,0175	0,9964
			VA7E	0,0230	0,0161	1,0000
			VA7F	0,0441	0,0184	0,9305
			VR11	0,0487	0,0197	0,8909
		LUM20	LP4BA	0,0186	0,0115	1,0000
			LUM10	0,0303	0,0198	1,0000
			LUM11	0,0329	0,0103	0,2201
			LUM12	0,0494	0,0128	0,0238
			LUM14	0,0604	0,0136	0,0021
			LUM16	0,0265	0,0113	0,9510
			LUM17	0,0337	0,0147	0,9680
			LUM18	0,0223	0,0198	1,0000
			LUM19	0,0053	0,0152	1,0000
			LUM3	0,0652	0,0139	0,0007
			LUM4	0,0316	0,0133	0,9397
			LUM7	0,0325	0,0136	0,9304
			LUM8	0,0067	0,0139	1,0000
			LUM9	0,0133	0,0184	1,0000
			VA7D	0,0419	0,0147	0,5289
			VA7E	0,0283	0,0130	0,9911
			VA7F	0,0494	0,0157	0,2699
			VR11	0,0540	0,0173	0,2798

Width M2 continued

		Localities	Localities	Mean Difference	Standard error	Significance
WIDTH M2	Hochberg	LUM3	LP4BA	-0,0465	0,0136	0,1137
			LUM10	-0,0349	0,0211	1,0000
			LUM11	-0,0323	0,0126	0,8250
			LUM12	-0,0157	0,0148	1,0000
			LUM14	-0,0048	0,0154	1,0000
			LUM16	-0,0387	0,0134	0,5016
			LUM17	-0,0315	0,0164	0,9998
			LUM18	-0,0429	0,0211	0,9984
			LUM19	-0,0599	0,0168	0,0718
			LUM20	-0,0652	0,0139	0,0007
			LUM4	-0,0336	0,0152	0,9854
			LUM7	-0,0326	0,0154	0,9952
			LUM8	-0,0585	0,0157	0,0399
			LUM9	-0,0519	0,0198	0,7638
			VA7D	-0,0233	0,0164	1,0000
			VA7E	-0,0369	0,0150	0,8903
			VA7F	-0,0158	0,0174	1,0000
			VR11	-0,0112	0,0188	1,0000
		LUM4	LP4BA	-0,0129	0,0130	1,0000
			LUM10	-0,0013	0,0207	1,0000
			LUM11	0,0013	0,0119	1,0000
			LUM12	0,0178	0,0142	1,0000
			LUM14	0,0288	0,0149	0,9997
			LUM16	-0,0051	0,0128	1,0000
			LUM17	0,0021	0,0159	1,0000
			LUM18	-0,0093	0,0207	1,0000
			LUM19	-0,0263	0,0163	1,0000
			LUM20	-0,0316	0,0133	0,9397
			LUM3	0,0336	0,0152	0,9854
			LUM7	0,0010	0,0149	1,0000
			LUM8	-0,0249	0,0152	1,0000
			LUM9	-0,0183	0,0193	1,0000
			VA7D	0,0103	0,0159	1,0000
			VA7E	-0,0033	0,0144	1,0000
			VA7F	0,0178	0,0169	1,0000
			VR11	0,0224	0,0183	1,0000
		LUM7	LP4BA	-0,0139	0,0133	1,0000
			LUM10	-0,0023	0,0209	1,0000
			LUM11	0,0004	0,0123	1,0000
			LUM12	0,0169	0,0145	1,0000
			LUM14	0,0279	0,0151	1,0000
			LUM16	-0,0061	0,0131	1,0000
			LUM17	0,0012	0,0161	1,0000
			LUM18	-0,0103	0,0209	1,0000
			LUM19	-0,0273	0,0166	1,0000
			LUM20	-0,0325	0,0136	0,9304
			LUM3	0,0326	0,0154	0,9952
			LUM4	-0,0010	0,0149	1,0000
			LUM8	-0,0258	0,0154	1,0000
			LUM9	-0,0193	0,0195	1,0000
			VA7D	0,0094	0,0161	1,0000
			VA7E	-0,0043	0,0147	1,0000
			VA7F	0,0168	0,0171	1,0000
			VR11	0,0214	0,0185	1,0000
		LUM8	LP4BA	0,0119	0,0136	1,0000
			LUM10	0,0235	0,0211	1,0000
			LUM11	0,0262	0,0126	0,9971
			LUM12	0,0427	0,0148	0,4861
			LUM14	0,0537	0,0154	0,0934
			LUM16	0,0198	0,0134	1,0000
			LUM17	0,0270	0,0164	1,0000
			LUM18	0,0155	0,0211	1,0000
			LUM19	-0,0015	0,0168	1,0000
			LUM20	-0,0067	0,0139	1,0000
			LUM3	0,0585	0,0157	0,0399
			LUM4	0,0249	0,0152	1,0000
			LUM7	0,0258	0,0154	1,0000
			LUM9	0,0065	0,0198	1,0000
			VA7D	0,0352	0,0164	0,9933
			VA7E	0,0215	0,0150	1,0000
			VA7F	0,0426	0,0174	0,8986
			VR11	0,0473	0,0188	0,8574

Width M2 continued

		Localities	Localities	Mean Difference	Standard error	Significance
WIDTH M2	Hochberg	LUM9	LP4BA	0,0054	0,0181	1,0000
			LUM10	0,0170	0,0242	1,0000
			LUM11	0,0197	0,0174	1,0000
			LUM12	0,0362	0,0190	0,9998
			LUM14	0,0471	0,0195	0,9230
			LUM16	0,0132	0,0180	1,0000
			LUM17	0,0205	0,0203	1,0000
			LUM18	0,0090	0,0242	1,0000
			LUM19	-0,0080	0,0207	1,0000
			LUM20	-0,0133	0,0184	1,0000
			LUM3	0,0519	0,0198	0,7638
			LUM4	0,0183	0,0193	1,0000
			LUM7	0,0193	0,0195	1,0000
			LUM8	-0,0065	0,0198	1,0000
			VA7D	0,0286	0,0203	1,0000
			VA7E	0,0150	0,0192	1,0000
			VA7F	0,0361	0,0211	1,0000
			VR11	0,0407	0,0223	1,0000
		VA7D	LP4BA	-0,0233	0,0144	1,0000
			LUM10	-0,0116	0,0216	1,0000
			LUM11	-0,0090	0,0135	1,0000
			LUM12	0,0075	0,0155	1,0000
			LUM14	0,0185	0,0161	1,0000
			LUM16	-0,0154	0,0142	1,0000
			LUM17	-0,0082	0,0171	1,0000
			LUM18	-0,0196	0,0216	1,0000
			LUM19	-0,0366	0,0175	0,9964
			LUM20	-0,0419	0,0147	0,5289
			LUM3	0,0233	0,0164	1,0000
			LUM4	-0,0103	0,0159	1,0000
			LUM7	-0,0094	0,0161	1,0000
			LUM8	-0,0352	0,0164	0,9933
			LUM9	-0,0286	0,0203	1,0000
			VA7E	-0,0136	0,0157	1,0000
			VA7F	0,0075	0,0180	1,0000
			VR11	0,0121	0,0194	1,0000
		VA7E	LP4BA	-0,0096	0,0127	1,0000
			LUM10	0,0020	0,0205	1,0000
			LUM11	0,0047	0,0117	1,0000
			LUM12	0,0212	0,0139	1,0000
			LUM14	0,0321	0,0147	0,9882
			LUM16	-0,0018	0,0125	1,0000
			LUM17	0,0055	0,0157	1,0000
			LUM18	-0,0060	0,0205	1,0000
			LUM19	-0,0230	0,0161	1,0000
			LUM20	-0,0283	0,0130	0,9911
			LUM3	0,0369	0,0150	0,8903
			LUM4	0,0033	0,0144	1,0000
			LUM7	0,0043	0,0147	1,0000
			LUM8	-0,0215	0,0150	1,0000
			LUM9	-0,0150	0,0192	1,0000
			VA7D	0,0136	0,0157	1,0000
			VA7F	0,0211	0,0167	1,0000
			VR11	0,0257	0,0181	1,0000
		VA7F	LP4BA	-0,0307	0,0155	0,9993
			LUM10	-0,0191	0,0223	1,0000
			LUM11	-0,0164	0,0146	1,0000
			LUM12	0,0001	0,0165	1,0000
			LUM14	0,0110	0,0171	1,0000
			LUM16	-0,0229	0,0153	1,0000
			LUM17	-0,0157	0,0180	1,0000
			LUM18	-0,0271	0,0223	1,0000
			LUM19	-0,0441	0,0184	0,9305
			LUM20	-0,0494	0,0157	0,2699
			LUM3	0,0158	0,0174	1,0000
			LUM4	-0,0178	0,0169	1,0000
			LUM7	-0,0168	0,0171	1,0000
			LUM8	-0,0426	0,0174	0,8986
			LUM9	-0,0361	0,0211	1,0000
			VA7D	-0,0075	0,0180	1,0000
			VA7E	-0,0211	0,0167	1,0000
			VR11	0,0046	0,0202	1,0000

Width M2 continued

		Localities	Localities	Mean Difference	Standard error	Significance
WIDTH M2	Hochberg	VR11	LP4BA	-0,0353	0,0170	0,9973
			LUM10	-0,0237	0,0234	1,0000
			LUM11	-0,0210	0,0163	1,0000
			LUM12	-0,0045	0,0180	1,0000
			LUM14	0,0064	0,0185	1,0000
			LUM16	-0,0275	0,0169	1,0000
			LUM17	-0,0203	0,0194	1,0000
			LUM18	-0,0317	0,0234	1,0000
			LUM19	-0,0487	0,0197	0,8909
			LUM20	-0,0540	0,0173	0,2798
			LUM3	0,0112	0,0188	1,0000
			LUM4	-0,0224	0,0183	1,0000
			LUM7	-0,0214	0,0185	1,0000
			LUM8	-0,0473	0,0188	0,8574
			LUM9	-0,0407	0,0223	1,0000
			VA7D	-0,0121	0,0194	1,0000
			VA7E	-0,0257	0,0181	1,0000
			VA7F	-0,0046	0,0202	1,0000

7. The lineage *M. bilbilis - M. ibericus*

7.1. INTRODUCTION

In this chapter, we focus on the group of the large-sized *Megacricetodon* from the middle and upper Miocene of the Calatayud-Montalbán Basin.

Freudenthal (1963) described in his thesis the species *Megacricetodon crusafonti* from the locality of Manchones in the Calatayud-Montalbán Basin. Moreover, he suggests the lineage *M. crusafonti - M. gregarious – M. ibericus.*

Afterwards, Daams & Freudenthal (1988a) in their work about the Iberian *Megacricetodon* distinguish the evolutionary lineage of *M. primitivus- ibericus.* In this lineage *M. primitivus* evolve to *M. collongensis*; this middle Aragonian species evolve to an intermediate stage *(M. collongensis-crusafonti*) during the upper Aragonian; which evolve to *M. crusafonti* in the local zone G2; there is an intermediate stage (*M. crusafonti-M. ibericus*) during the biozone G3; and finally during lower Vallesian occurs *M. ibericus* (Table 7.1). Both *Megacricetodon collongensis-crusafonti* and *M. crusafonti-M. ibericus* are considered as intermediate evolutionary stages and not as a new species. These authors show the variation in the character states of this lineage and the evolutionary trends in size and morphology throughout time. However, they noted some discontinuity in the hypothetical *M. primitivus- ibericus* lineage, both in size and morphology, especially in the older species of the lineage.

Daams et al. (1999) considered that the intermediate stage *Megacricetodon collongensis-crusafonti* has magnitude enough to be treated as a species and was assigned to *M. gersii* (see Table 7.1).

Based on our comparative study, the representatives classified as *Megacricetodon collongensis-crusafonti* are different from *Megacricetodon gersii* which occurs in the upper part of local zone Dd and E, and can be clearly distinguished from from *M. crusafonti* and *M. ibericus*. These differences are enough to consider this form as a new species (Table 7.1).

Therefore, the aim of this chapter is characterizes the species of the upper part of the local zone E and zones F and G1, as well as, make clear the lineage *Megacricetodon crusafonti*.

Objectives of the chapter:

- Describe and characterize the *Megacricetodon* species from the upper part of the local zone E, F and G1.

- Describe and define the the large sized *Megacricetodon* lineage recorded from the middle and upper Miocene in the Calatayud-Montalbán Basin (local zones E, F, G1, G2, G3 and H).

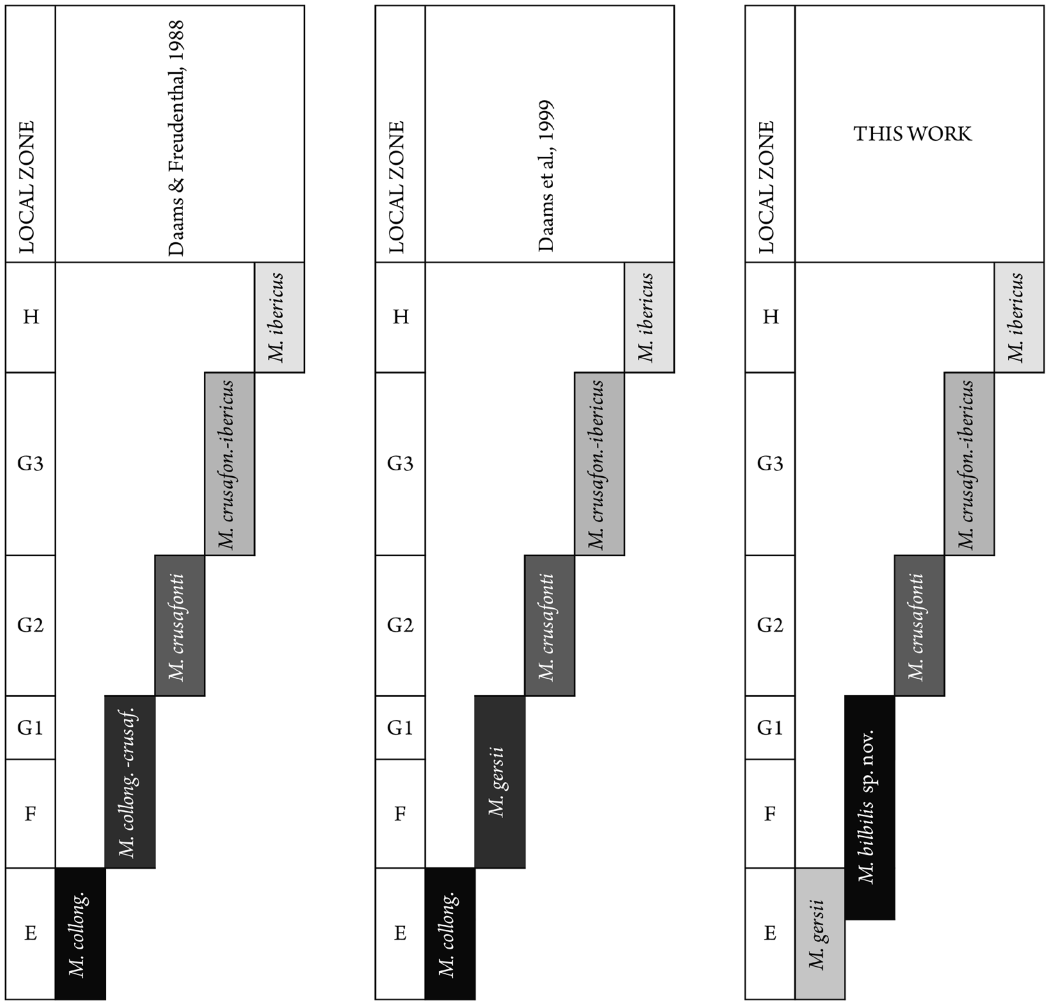


Table 7.1. History of the "*Megacricetodon crusafonti* lineage" in the Calatayud-Montalbán Basin.

7.2. MATERIAL

In order to characterize this *Megacricetodon* lineage, new material not published before from seven localities of the Calatayud-Montalbán Basin has been studied: Las Umbrias 18, Las Umbrias 19, Las Umbrias 20, Las Umbrias 22, Las Planas 5B, Valalto 1A and Valalto 1B. Material from all those localities is stored at the Museo Nacional de Ciencias Naturales, CSIC (Madrid, Spain). Classical collections published by Daams & Freudenthal (1988a) from Las Planas 5B, Valalto 1A and Valalto 1B are stored in the Nationaal Natuurhistorisch Museum-Naturalis (Leiden, The Netherlands).

In addition, data of *Megacricetodon* published by Daams & Freudenthal (1988a) from the localities of Las Planas 4A, Armantes 7, Valalto 2B, Valalto 2C, Las Planas 5B, Las Planas 5C, Borjas, Las Planas 5L, Las Planas 5K, Villafeliche 9, Alcocer 2, Las Planas 5H, Toril 1, Solera and Carrilanga 1 have been included for the morphometric comparisons and analyses.

7.3. SYSTEMATIC PALAEONTOLOGY

Order RODENTIA Bowdich, 1821
Family MURIDAE Illiger, 1811
Subfamily CRICETODONTINAE Schaub, 1925
Genre *Megacricetodon* Fahlbusch, 1964
Megacricetodon bilbilis sp. nov.
(Figs. 7.1: A–K)

Megacricetodon collongensis-crusafonti from Valalto 2B, Valalto 2C, Las Planas 5B and Valato 1 in Daams et al., 1987: 304, fig. 5.

Megacricetodon gersii García Moreno, 1987: 55-61, 100-101.

Megacricetodon collongensis-crusafonti from Valalto 2B, Valalto 2C, Las Planas 5B and Valalto 1 in Daams & Freudenthal, 1988b: 14, fig. 8.

Megacricetodon gersii Daams et al., 1998: 626-627, fig. 1.

Megacricetodon gersii from F and G1 in Daams et al., 1999: 126, fig. 10, 127.

Megacricetodon gersii-ibericus from F and G1 in Alcalá et al., 2000: 327, fig. 3.

Megacricetodon gersii from F in López Olmedo et al., 2004

Megacricetodon gersii Álvarez-Sierra et al., 2006: 7-8, plate 1 fig. 7.

Megacricetodon gersii Hernández Fernández et al., 2006: 282.

Megacricetodon "gersii" Hernández-Ballarín et al., 2011: 176-180, tabla 1, fig. 3.

Megacricetodon collongensis-crusafonti Sesé & Jiménez Rodrigo, 2014: 12-18, table 1, fig. 4, 5.

Diagnosis: Large-sized species of *Megacricetodon*. Upper first molar with anterocone always double, normally with a platform or a strong anterior cingulum in front of it; mesoloph normally short. In the lower first molar the anteroconid is double (slightly subdivided or 8-shaped) between the 35-65% of the specimens; mesolophids of short length in m1 and m2.

Differential Diagnosis: *Megacricetodon bilbilis* sp. nov. differs from the small and the medium-sized group of *Megacricetodon* defined by Peláez-Campomanes & Daams (2002) and Oliver & Peláez-Campomanes (2013) by its larger dimensions.

Megacricetodon bilbilis sp. nov. has the same size than *M. crusafonti* (Freudenthal, 1963) and *M. ibericus* (Schaub, 1944). However, differ with them in the less subdivided anteroconid of the m1 (never is deeply split).

Megacricetodon bilbilis sp. nov. differs from *M. aunayi* Lazzari & Aguilar, 2007, *M. fahlbuschi* Aguilar et al., 1999, *M. fournasi* Aguilar, 1995, *M. germanicus* Aguilar, 1980,

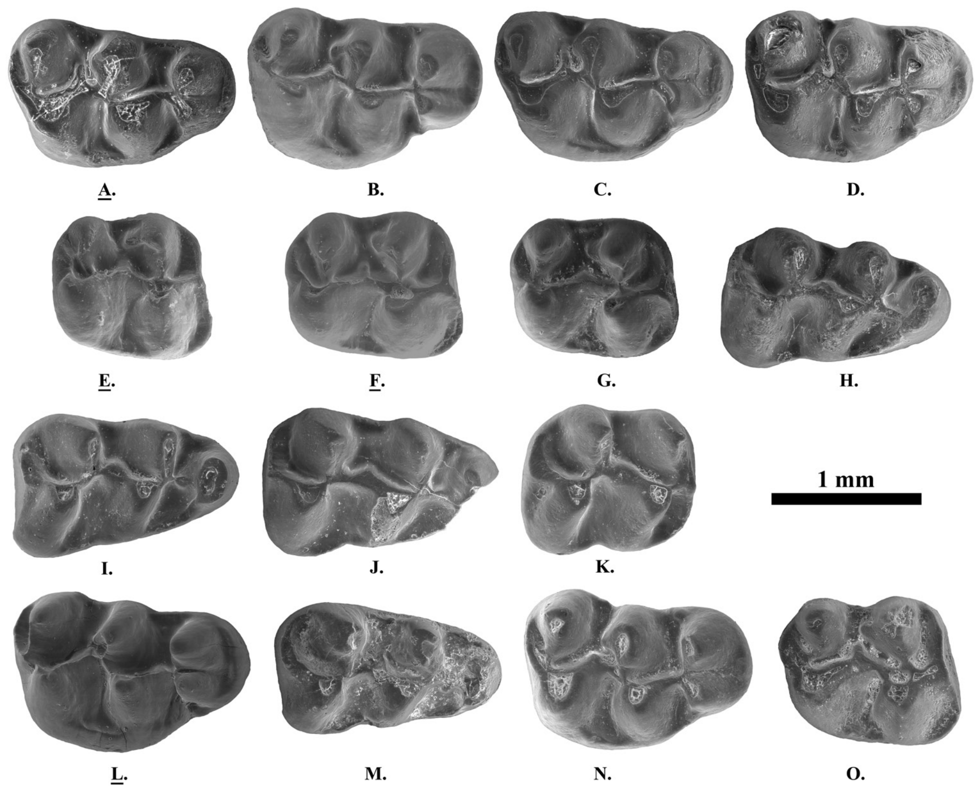


Figure 7.1. *Megacricetodon bilbilis* sp. nov. from the Calatayud-Montalbán Basin. Las Umbrias 22 (type locality): A, M1 left LUM22-13; B, M1 right LUM22-25; C, M1 right LUM22-27; D, M1 right LUM22-28; E, M2 left LUM22-40; F, M2 left LUM22-45; G, M2 right LUM22-63; H, m1 right LUM22-78; I, holotype m1 right LUM22-81; J, m1 right LUM22-84; K, m2 right LUM22-112. Las Umbrias 18: L, M1 left LUM18-54. Las Umbrias 19: M, m1 right LUM19-241. Las Umbrias 20: N, M1 right LUM20-57; O, M2 right LUM20-102. All specimens are figured as right; left ones are indicated by underlined label. All of the teeth are at the same magnification. Scale bar equals 1 mm.

M. gregarius (Schaub, 1925), *M. lappi* (Mein, 1958), *M. roussillonensis* Aguilar et al., 1986 and *M. wae* Aguilar et al., 1999, by its smaller size.

Megacricetodon bilbilis sp. nov. differs from *M. bezianensis* Bulot, 1980, *M. bourgeoisi* (Schaub, 1925), *M. gersii* Aguilar, 1980, *M. lalai* Aguilar et al., 1999, *M. robustus* Kälin & Engesser, 2001, *M. vandermeuleni* Oliver & Peláez-Campomanes, 2013, by its larger size.

Megacricetodon bavaricus (Fahlbusch, 1964) is similar in size to *M. bilbilis* sp. nov., however, they differ by having a "crescent"-shaped anteroconid and a the slightly subdivided anterocone of the M1.

Megacricetodon lemartinelli Aguilar, 1995 has similar size to *M. bilbilis* sp. nov., nevertheless, they differ by having the m1 with higher percentage of simple and elongated anteroconid and larger mesolophid; M1 with higher percentage of slightly subdivided anterocone and larger mesoloph; and M2 with higher percentage of anterior protolophule.

Holotype: m1 dext, LUM22-81 (Fig. 7.1 I).

Etymology: The *Megacricetodon* from the Calatayud (Bilbilis) Basin.

Type Locality: Las Umbrias 22 (Spain).

Paratype: LUM22–0.3, LUM22–0.7, LUM22–1.5, LUM22–2, LUM22–2.1, LUM22–3.6, LUM22–3.7, LUM22–4.5, LUM22–5, LUM22–6.3, LUM22–6.6, LUM22–6.8, LUM22–6.9, LUM22–8.2 to LUM22–8.5, LUM22–12, LUM22–13, LUM22–18, LUM22–20, LUM22–23, LUM22–25 to LUM22–28, LUM22–31 to LUM22–34, LUM22–37 to LUM22–40, LUM22–44 to LUM22–55, LUM22–58, LUM22–61 to LUM22–65, LUM22–68 to LUM22–80, LUM22–84, LUM22–86 to LUM22–88, LUM22–91, LUM22–92, LUM22–96 to LUM22–108, LUM22–110 to LUM22–113.

Other Localities: Las Umbrias 18 (Figs. 7.1 L), Las Umbrias 19 (Figs. 7.1 M), Las Umbrias 20 (Figs. 7.1 N,O), Las Planas 4A, Armantes 7, Valalto 2B, Valalto 2C, Las Planas 5B, Las Planas 5C, Valalto 1A and, Valalto 1B.

Stratigraphical distribution: Uppermost part of local zone E (middle Aragonian, middle Miocene) to local zone G1 (upper Aragonian, middle Miocene).

Geographical distribution: Spain.

Measurements: Tables 7.2-7.3.

7.4. DESCRIPTION OF THE TYPE MATERIAL

M1: The anterocone is deeply split in all the specimens, of which four have a small platform in front of the furrow and four a small cingulum ridge in front of it. One out of 12 has an incipient forward paracone spur. The protolophule is always posterior. The ectoloph is strong in four specimens, short in seven, and absent in one. The mesoloph is short in 11 out of 12 and absent in one. In 10 out of 12, there is no connection between the ectoloph and the mesoloph, in one there is a mesoloph but the ectoloph is absent and in the remaining one there is neither a mesoloph nor an ectoloph. The metalophule is connected to the posteroloph just behind the hypocone in one, is posterior and the metalophule points backwards in six, and is posterior and the metalophule points backwards more obliquely delimiting a small posterosinus in one (see Appendix 7.1).

Species	Element	Sites	T. N.	N.	min	mean	max	σ	N.	min	mean	max	σ
			Length						Width				
M. ibericus		CAR1		21	1,62	1,73	1,9	0,07	21	0,96	1,1	1,23	0,06
M.crusafonti-ibericus		SOL		254	1,53	1,76	2	0,09	290	0,91	1,12	1,3	0,06
M.crusafonti-ibericus		TOR1		101	1,6	1,77	1,99	0,08	120	0,95	1,12	1,28	0,05
M.crusafonti-ibericus		LP5H		46	1,58	1,77	1,95	0,1	58	0,93	1,11	1,25	0,07
M.crusafonti-ibericus		AC2		29	1,48	1,63	1,87	0,1	43	0,85	1,01	1,22	0,08
M.crusafonti-ibericus		VL9		87	1,55	1,77	1,96	0,08	102	1	1,12	1,25	0,06
M.crusafonti		LP5K		15	1,5	1,72	1,87	0,1	19	0,96	1,09	1,23	0,08
M.crusafonti		LP5L		15	1,57	1,76	1,87	0,1	16	0,96	1,11	1,23	0,07
M.crusafonti		BOR		99	1,52	1,71	1,95	0,08	113	0,93	1,08	1,28	0,06
M.crusafonti		MAN		260	1,54	1,76	2		260	0,94	1,1	1,26	
M. bilbilis	**M1**	VT1B	13	5	1,74	1,79	1,85	0,04	6	1	1,04	1,22	0,09
M. bilbilis		VT1A		7	1,63	1,7	1,8	0,06	8	1	1,06	1,11	0,04
M. bilbilis		LP5C		28	1,56	1,75	1,89	0,07	36	0,99	1,1	1,18	0,05
M. bilbilis		LP5B	83	34	1,62	1,77	1,93	0,07	46	0,98	1,04	1,21	0,06
M. bilbilis		VT2C		70	1,61	1,76	1,9	0,07	97	0,98	1,12	1,21	0,05
M. bilbilis		VT2B		17	1,64	1,75	1,89	0,07	25	1,01	1,1	1,21	0,05
M. bilbilis		ARM7		137	1,58	1,73	1,89		137	0,99	1,1	1,25	
M. bilbilis		LUM21	98	51	1,66	1,81	1,94	0,06	72	1,05	1,16	1,31	0,05
M. bilbilis		LUM22	18	7	1,7	1,74	1,8	0,04	10	1,04	1,1	1,2	0,05
M. bilbilis		LUM20	1	1		1,66			1		1		
M. bilbilis		LP4A		1		1,87			1		1,15		
M. bilbilis		LUM18	1	1		1,69			1		1		
M. ibericus		CAR1		13	1,14	1,23	1,31	0,05	14	0,97	1,09	1,15	0,05
M.crusafonti-ibericus		SOL		125	1,1	1,25	1,41	0,07	127	0,97	1,08	1,19	0,05
M.crusafonti-ibericus		TOR1		106	1,05	1,21	1,39	0,07	108	0,91	1,06	1,23	0,06
M.crusafonti-ibericus		LP5H		38	1,08	1,24	1,45	0,09	38	0,92	1,05	1,16	0,06
M.crusafonti-ibericus		AC2		20	1,06	1,17	1,34	0,08	19	0,89	1	1,09	0,06
M.crusafonti-ibericus		VL9		97	1,1	1,24	1,37	0,06	95	0,94	1,07	1,18	0,05
M.crusafonti		LP5K		25	1,09	1,23	1,45	0,1	24	0,93	1,08	1,24	0,08
M.crusafonti		LP5L		19	1,1	1,23	1,31	0,06	20	0,97	1,06	1,15	0,06
M.crusafonti	**M2**	BOR		118	1,09	1,21	1,38	0,06	119	0,94	1,06	1,2	0,05
M.crusafonti		MAN		179	1,04	1,18	1,33		179	0,92	1,07	1,23	
M. bilbilis		VT1B	13	3	1,18	1,22	1,25		3	1	1,03	1,08	
M. bilbilis		VT1A		5	1,11	1,17	1,2	0,04	5	1,01	1,06	1,12	0,04
M. bilbilis		LP5C		35	1,14	1,25	1,35	0,05	35	1	1,06	1,16	0,05
M. bilbilis		LP5B	86	43	1	1,22	1,39	0,08	48	0,9	1,04	1,17	0,04
M. bilbilis		LUM22	20	17	1,15	1,23	1,31	0,05	17	1,02	1,08	1,18	0,04
M. bilbilis		LUM20	1	1		1,31			1		1		
M. bilbilis		LP4A		1		1,23			1		1,06		
M. ibericus		CAR1		1		0,92			1		0,9		
M.crusafonti-ibericus		SOL		29	0,77	0,89	1		29	0,78	0,88	0,97	
M.crusafonti-ibericus		TOR1		29	0,82	0,9	0,97		30	0,8	0,88	0,99	
M.crusafonti-ibericus		LP5H		25	0,79	0,87	0,98		26	0,76	0,86	0,94	
M.crusafonti-ibericus		AC2		15	0,76	0,85	0,94		15	0,72	0,85	0,96	
M.crusafonti-ibericus		VL9		47	0,73	0,86	0,94		47	0,77	0,87	0,97	
M.crusafonti	**M3**	LP5K		10	0,77	0,81	0,89		8	0,78	0,82	0,85	
M.crusafonti		LP5L		12	0,82	0,86	0,91		11	0,78	0,85	0,97	
M.crusafonti		AV6		42	0,75	0,85	0,95		40	0,75	0,86	0,97	
M.crusafonti		BOR		60	0,71	0,85	0,94		60	0,75	0,85	0,99	
M.crusafonti		MAN		110	0,68	0,85	0,97		110	0,74	0,85	1,02	
M. bilbilis		VT1		7	0,75	0,83	0,95		7	0,8	0,86	0,92	
M. bilbilis		LP5B		6	0,76	0,83	0,95		6	0,8	0,88	0,96	
M. bilbilis		LUM22		15	0,8	0,87	0,95	0,04	15	0,81	0,87	0,95	0,04

Table 7.2. Descriptive statistics of the upper molars of the lineage *Megacricetodon bilbilis – M. crusafonti – M. crusafonti-ibericus – M. ibericus* from the Calatayud-Montalbán Basin. Abbreviations: T.N., total number of teeth; N., number of teeth measured; min, minimum; max, maximum; δ, standard deviation.

Species	Element	Sites	T. N.	Length					Width				
				N.	min	mean	max	σ	N.	min	mean	max	σ
M. ibericus		CAR1		22	1,54	1,63	1,78	0,06	24	0,87	1	1,11	0,05
M.crusafonti-ibericus		SOL		165	1,49	1,67	1,91	0,09	180	0,84	1,01	1,15	0,06
M.crusafonti-ibericus		TOR1		107	1,49	1,65	1,85	0,07	144	0,9	1,02	1,18	0,05
M.crusafonti-ibericus		LP5H		33	1,51	1,67	1,9	0,1	42	0,83	1,01	1,18	0,07
M.crusafonti-ibericus		AC2		17	1,47	1,59	1,72	0,09	28	0,78	0,97	1,09	0,08
M.crusafonti-ibericus		VL9		99	1,48	1,65	1,92	0,07	107	0,88	1,01	1,15	0,05
M.crusafonti		LP5K		9	1,53	1,64	1,74	0,07	10	0,88	0,95	1,01	0,03
M.crusafonti		LP5L		30	1,53	1,67	1,83	0,08	31	0,91	1,01	1,17	0,07
M.crusafonti		BOR		104	1,45	1,63	1,81	0,07	118	0,83	0,98	1,14	0,06
M.crusafonti		MAN		238	1,47	1,66	1,92		238	0,87	1	1,18	
M. bilbilis	**m1**	VT1B	11	1		1,75			5	0,96	1,05	1,08	0,05
M. bilbilis		VT1A	7	6	1,49	1,53	1,59	0,04	7	0,9	0,93	0,98	0,03
M. bilbilis		LP5C		25	1,54	1,64	1,76	0,07	27	0,86	0,98	1,05	0,05
M. bilbilis		LP5B	102	38	1,53	1,64	1,75	0,06	49	0,91	0,98	1,06	0,03
M. bilbilis		VT2C		85	1,45	1,61	1,82	0,07	100	0,89	1,01	1,11	0,04
M. bilbilis		VT2B		14	1,5	1,57	1,65	0,05	22	0,91	0,99	1,12	0,04
M. bilbilis		ARM7		119	1,48	1,6	1,74		118	0,9	0,98	1,08	
M. bilbilis		LUM22	19	10	1,57	1,67	1,79	0,07	12	0,98	1,03	1,1	0,04
M. bilbilis		LP4C		1		1,6			1		1,01		
M. bilbilis		LUM19	1	1		1,66			1		0,97		
M. ibericus		CAR1		21	1,14	1,23	1,36	0,07	21	0,88	1,04	1,13	0,05
M.crusafonti-ibericus		SOL		193	1,09	1,25	1,43	0,07	202	0,89	1,05	1,18	0,06
M.crusafonti-ibericus		TOR1		123	1,09	1,25	1,49	0,06	133	0,91	1,04	1,19	0,06
M.crusafonti-ibericus		LP5H		39	1,09	1,26	1,43	0,09	50	0,92	1,04	1,19	0,07
M.crusafonti-ibericus		AC2		23	1,07	1,18	1,38	0,09	29	0,86	1	1,17	0,1
M.crusafonti-ibericus		VL9		122	1,08	1,26	1,39	0,05	120	0,91	1,04	1,17	0,05
M.crusafonti		LP5K		19	1,13	1,27	1,51	0,09	23	0,89	1,03	1,16	0,07
M.crusafonti	**m2**	LP5L		25	1,16	1,29	1,42	0,06	26	0,98	1,05	1,13	0,05
M.crusafonti		BOR		116	1,1	1,23	1,42	0,06	122	0,89	1,01	1,19	0,06
M.crusafonti		MAN		250	1,11	1,27	1,44		250	0,9	1,05	1,19	
M. bilbilis		VT1B	12	2	1,29	1,31	1,32		4	1	1,02	1,07	
M. bilbilis		VT1A	9	8	1,17	1,2	1,23	0,02	9	0,89	0,97	1,07	0,05
M. bilbilis		LP5C		37	1,19	1,27	1,33	0,04	39	0,94	1,03	1,13	0,04
M. bilbilis		LP5B	90	41	1	1,25	1,41	0,08	51	0,93	1,01	1,08	0,04
M. bilbilis		LUM22	18	10	1,22	1,26	1,32	0,03	13	1	1,06	1,15	0,05
M. bilbilis		LUM19	1	1		1,26			1		1,08		
M. ibericus		CAR1		3	1,07	1,09	1,11		3	0,89	0,93	0,98	
M.crusafonti-ibericus		SOL		57	0,91	1,06	1,26		57	0,75	0,89	1,03	
M.crusafonti-ibericus		LP5H		35	0,97	1,09	1,25		43	0,75	0,87	1,02	
M.crusafonti-ibericus		AC2		15	0,94	1,02	1,13		17	0,76	0,85	0,94	
M.crusafonti-ibericus		VL9		65	0,89	1,05	1,16		68	0,76	0,86	0,96	
M.crusafonti		LP5K		18	1	1,09	1,28		18	0,75	0,89	1,08	
M.crusafonti	**m3**	LP5L		15	0,99	1,07	1,16		14	0,79	0,87	0,92	
M.crusafonti		AV6		61	0,88	1,04	1,15		58	0,74	0,86	0,98	
M.crusafonti		BOR		71	0,91	1,05	1,22		82	0,72	0,86	0,99	
M.crusafonti		MAN		158	0,88	1,04	1,2		158	0,7	0,86	1,01	
M. bilbilis		VT1		4	1	1,08	1,15		5	0,89	0,92	0,97	
M. bilbilis		LP5B		35	0,92	1,04	1,17		36	0,78	0,87	0,99	
M. bilbilis		LUM22		15	1	1,04	1,12	0,04	15	0,79	0,86	0,96	0,04

Table 7.3. Descriptive statistics of the lower molars of the lineage *Megacricetodon bilbilis – M. crusafonti – M. crusafonti-ibericus – M. ibericus* from the Calatayud-Montalbán Basin. Abbreviations: T.N., total number of teeth; N., number of teeth measured; min, minimum; max, maximum; δ, standard deviation.

M2: The protolophule is anterior in two specimens, is transverse in one, it is transverse but connected to the entoloph behind the protocone in two, it is connected to the protocone indirectly through the paracone and protolophule in five and it is double in six. In 17 out of 18 the ectoloph is strong and in one it is short. The mesoloph is long in one, medium in one, short in 10 and absent in five specimens. The ectoloph is connected with the mesoloph in three, there is no connection between the ectoloph and the mesoloph in nine, and there is an ectoloph but the mesoloph is absent in five. The metalophule is anterior (6/16), anterior almost double (1/6), transverse (1/16), points backwards and it is connected to the posteroloph, just behind the hypocone (2/16), the metalophule is more oblique reducing the posterosinus (4/16) or double (2/16) (Appendix 7.1).

M3: The lingual anteroloph is absent in seven, incipient in five and well developed in two specimen. The labial anteroloph and the paracone are always well developed. The mesoestyl is present in two out of 14, incipient in one out of 14 or absent in 11 out of 14. The metalophule is absent (7/13), or it is connected to the neo-entoloph (4/13), or it is connected to the anterior arm of the hypocone (1/13), or it is connected to the protolophule and the anterior arm of the hypocone (1/13).

m1: The anteroconid is rounded, being simple in five specimens, slightly subdivided in two and 8-shaped in one. The metalophulid is always anteriorly connected. The mesolophid is short (3/13) or absent (10/13) (see Appendix 7.1).

m2: The lingual anterolophulid is long (1/11), short (8/11) or absent (2/11). The labial mesocingulid is present in 16 and incipient in one specimen. The mesolophid is of short (8/19) or absent (11/19) (Appendix 7.1).

m3: The lingual anterolophulid is long in one out of 12, short in 10 out of 12 an absent in one out of 12. The labial mesocingulid is absent (5/15), incipient (1/15) or well developed (9/15). The mesolophid is always absent.

7.5. RESULTS AND DISCUSSION

All the assemblages of *Megacricetodon bilbilis* sp. nov. from the Calatayud-Montalbán Basin are similar in morphology and dimensions (see Appendix 7.1 and Tables 7.2-7.3).Only the material of *Megacricetodon* from Las Planas 5B shows small differences with the type material of Las Umbrias 22. These data, taken from Daams & Freudenthal, (1988a), have not been revised by us. Studying their scatter diagrams and the morphotype distribution of the two *Megacricetodon* species found in LP5B it is possible that the differences in character state proportions are due to the inclusion of some *M.*

minor representatives within their *M. collongensis-crusafonti* sample (See Appendix 7.1 Tables 8, 12, 17).

Megacricetodon bilbilis sp. nov. is characterized by upper first molar with a well subdivided anterocone, normally with a platform or a strong anterior cingulum in front of it, ectoloph variable, metalophule posterior (connected to the posteroloph just behind the hypocone or points backwards), short or medium mesolophs in the upper molars (M1 and M2), strong ectoloph and variable protolophule in the M2; lower first molar with presence of anteroconid double (slightly subdivided or 8-shaped) between the 35-65% of the specimens, mesolophids of short length in m1 and m2, and short or absent lingual anterolophid in the m2 (Appendix 7.1).

This new species is larger than older *Megacricetodon* assemblages from the Iberian Peninsula, such as *M. vandermeuleni* and the species from the *M. primitivus* group (*M. primitivus*, *M. alvarezae*, *M. collongensis* and *M. gersii*). The *Megacricetodon* material from the local zones F and G1 had been assigned to *M. gersii* (Daams et al., 1999), after the description and discussion of new material from the Calatayud-Montalbán Basin included in Chapter 6 we propose that the distribution of the species *Megacricetodon gersii* is restricted to the upper part of zone Dd and zone E. Whereas, this new species has its first occurrence in the upper part of zone E (co-occurring with *M. gersii*) and remains till local zone G1, when evolves into *M. crusafonti*.

This new species differs from the younger representatives of its *Megacricetodon* lineage from the Calatayud-Montalbán Basin (*M. crusafonti*, *M. crusafonti-ibericus* and *M. ibericus*) by the degree of the subdivided anteroconid of the lower first molar, that in *M. bilbilis* sp. nov. is never deeply split (Appendix 7.1).

The lineage Megacricetodon bilbilis – M. ibericus

The assemblages included in *Megacricetodon bilbilis* sp. nov. from the Calatayud-Montalbán Basin share dental morphologies and size with the assemblages assigned to *M. crusafonti*, *M. crusafonti-ibericus* and *M. ibericus*. Therefore we corroborate the inclusion of this species in the lineage leading *M. ibericus* proposed by Daams & Freudenthal (1988a) as the earliest form distinguished in the Basin. All this *Megacricetodon* forms are characterised by upper first molars having well subdivided the anterocone, normally with a platform or a strong anterior cingulum in front of it, short or absent mesoloph, posterior metalophule; M2 with protolophule connections highly variable; lower first molar with double anteroconid , mesolophids short or absent in m1 and m2, and short or absent lingual anterolophid in the m2.

In the following paragraphs we discuss the *Megacricetodon* assemblages from different Spanish and European basins that have been assigned to *M. collongensis-crusafonti* or *M. gersii*, that could be assigned to *Megacricetodon bilbilis* sp. nov., or to other species of this lineage.

Duero Basin: García Moreno (1987) assigned to *M. gersii* the material from Valladolid 1. We do not agree with this allotment considering that both the size and the morphology are closer to the *Megacricetodon bilbilis* sp. nov.

Ebro Basin: The *Megacricetodon* material from the locality of Melero 30 has been correlated to local zone F-G1 and assigned to *Megacricetodon collongensis-crusafonti* (Murelaga et al., 2008). The morphology and size of the material is compatible with its assignation to *M. bilbilis* sp. nov.

Madrid Basin: The *Megacricetodon* from the localities of Henares 1, Paracuellos 3 and Paracuellos 5 was studied by Alberdi et al., (1981); López Martínez et al., (1983); Sesé et al., (1985) and López et al., (1987) and assigned to *M. crusafonti*. Afterwards Herráez (1993) in her thesis assigned to *M. gersii* the material from Henares 1 and Paracuellos 5. However, the size and morphology of these *Megacricetodon* assemblages allow us to consider them *M. bilbilis* sp. nov. Sesé & Jiménez Rodrigo (2014) described *M. collongensis-crusafonti* from Leganés. Based on the dimensions and morphology of this material we assigned it to. *M. bilbilis* sp. nov.

Vallés-Penedés Basin: Agustí et al., (1985) preliminary assigned to *M. crusafonti* the material from the locality of Les Conilleres. Based on the scarce information published (only the faunal list) it is not possible to decide on the taxonomic assignation of this material.

Levante basins: Ruiz-Sánchez et al., (2005) assigned to *Megacricetodon crusafonti* the material from the locality of Cazuma 1 (Quesa-Bicorp basin). We agree with this allotment based on the size and morphology of the *Megacricetodon* material.

Portugal basins: The *Megacricetodon* material from the localities of Póvoa de Santarém, Pero Filho and Chões were assigned to *M. crusafonti* by Antunes & Mein (1977). We agree in this allotment based on the size and morphology of the *Megacricetodon* material.

France basins: In the karstic site of Castelnou 6 Aguilar et al., (1994), described two species of *Megacricetodon*, *M. gersii* and *M.* cf. *crusafonti*. We agree in the assignation of these species based on the size and the morphology of them. However, despite the authors assigned the locality to an MN6 age, we thought that owing to the karstic origin of the site it is not possible to determinate the age correctly, considering that there might have been a mixture of levels. The faunal assemblage of the locality (*Megacricetodon* cf. *crusafonti, M. gersii, Cricetodon* sp., *Hispanomys castelnovi, Democricetodon* sp., *D*. cf. *crusafonti, D*. aff. *affinis, Muscardinus thaleri, Miodyromys* sp., *Heteroxerus* cf. *rubricati, Spermophilinus bredai*) suggest an age equal or younger to MN6.

In addition to the morphological differences pointed out between *M. gersii* and *M. bilbilis* sp. nov., the record of this two species together in the several localities in the Calatayud-Montalbán Basin (such as Las Umbrias 18, Las Umbrias 19, Las Planas 4A and Las Umbrias 20) and the possible co-occurrence of both species, in France, in the karstic locality of Castelnou 6 (Aguilar et al., 1994) impede to consider *M. gersii* as part of this lineage as proposed by Garcia Moreno (1987) and Daams et al., (1999) (see Table 7.1).

Therefore, the lineage *Megacricetodon bilbilis – M. ibericus* has its first occurrence in Spain, in the upper part of the local zone E (MN 5), with the species *Megacricetodon bilbilis* sp. nov. Throughout the time spam of this species 700 ka (from ~14 Ma LUM18 to ~13.3 Ma VT1B) co-occurred with *M. gersii* (in the upper part of the biozone E) and with the medium-sized *M. rafaeli* (local zone F), but keeping without changes in dimensions and morphology.

During local zone G1, *Megacricetodon bilbilis* sp. nov. is recorded with *Megacricetodon minor*, considering that evolves into *M. crusafonti* which is the representative recorded in the biozone G2.

During G3 (MN 7/8) occurred an intermediate *Megacricetodon* stage, *M. crusafonti-ibericus*, which finally evolves into *M. ibericus* in the early Vallesian (local zone H).

This lineage keeps its size without much variation from its first occurrence ~14 Ma (local zone E) to its last occurrence ~11.570 Ma (local zone H) (see Tables 7.2-7.3 and Figure 7.2). The main changes on which the lineage is build are in morphology. The trends shown by the *Megacricetodon bilbilis – M. ibericus* lineage are towards a reduction of mesolophs(ids), metalophule more backwards directed, implying a progressively less-developed posterosinus, in the M1, progressive subdivision of the anteroconid and a reduction of the lingual anterolophid in the m2.

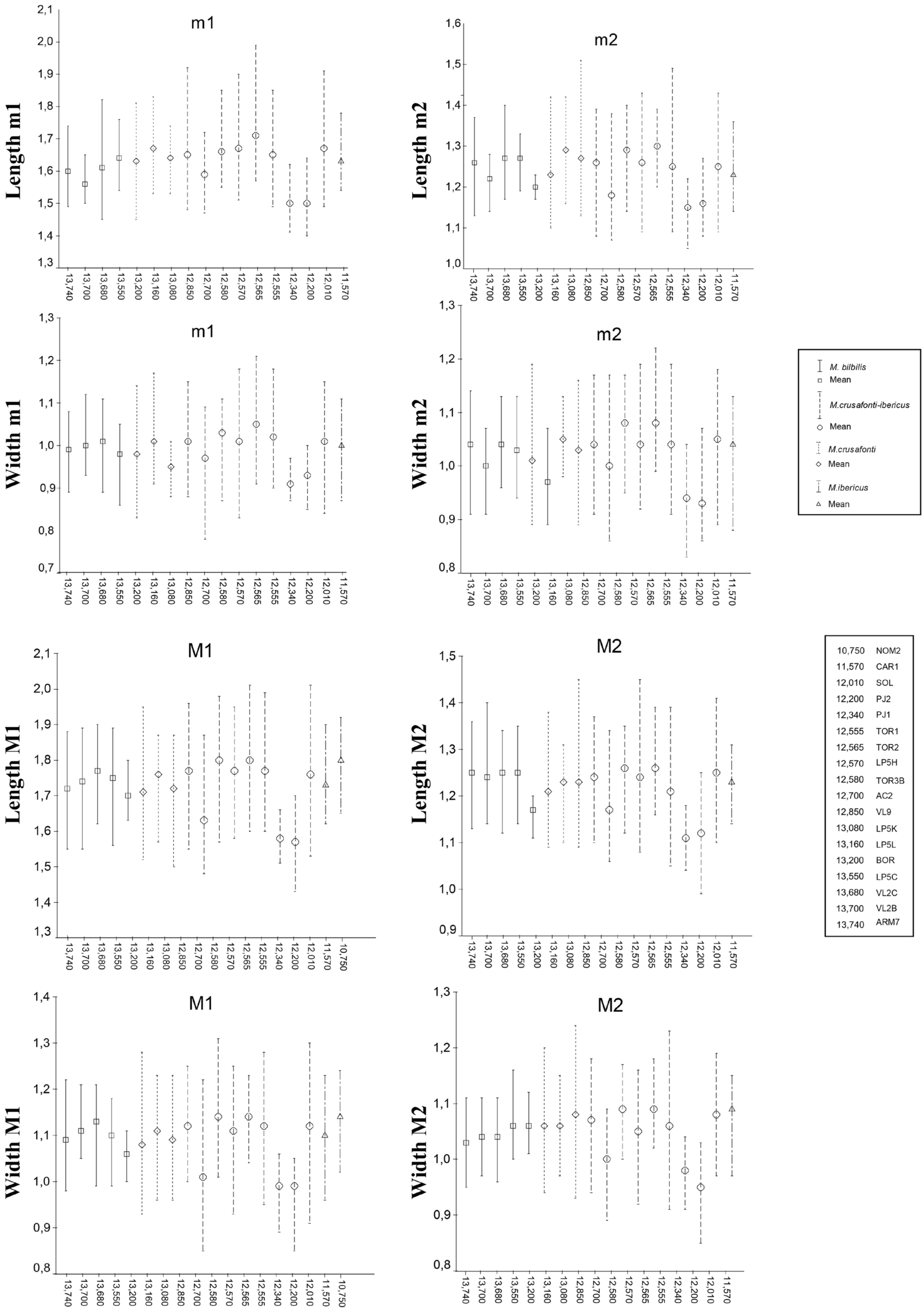


Figure 7.2. Distribution of the Length and Width ranges charts of the upper and lower dental elements for the successive assemblages of the lineage *Megacricetodon bilbilis-M. ibericus* from the Calatayud-Montalbán Basin.

7.6. CONCLUSIONS

The study and revision of the *Megacricetodon* material from the new and already known localities of the middle and upper Aragonian from the Calatayud-Montalbán Basin, allowed us to propose a new species, *Megacricetodon bilbilis* sp. nov. distributed in the biozones E, F, and G1.

We propose this new species as part of the lineage *Megacricetodon bilbilis – M. crusafonti - M. crusafonti-ibericus – M. ibericus*s.

Megacricetodon gersii has been excluded of the lineage *Megacricetodon bilbilis – M. ibericus.* In addition to the important morphological and metrical differences found between them, the exclusion of the former species from this lineage is based on their co-occurrence, since it is the first time that *M. gersii* and *M. bilbilis* sp. nov. have been unambiguously recorded together.

7.7. REFERENCES

Aguilar, J. 1980. Nouvelle interpretation de l'evolution du genre *Megacricetodon* au cours du Miocene. Paleovertebrata Volumen Jubilaire R. Lavocat:355-366.

Aguilar, J. P. 1995. Evolution de la lignée *Megacricetodon collongensis-Megacricetodon rousillonensis* (Cricetidae, Rodentia, Mammalia) au cours du Miocène inférieur et moyen dans le sud de la France. Palaeovertebrata 24:1-45.

Aguilar, J. P., M. Calvet, and J. Michaux. 1986. Découvertes de faunes de micromammifères dans les Pyrénées Orientales (France) de l'Oligocène supérieur au Miocène supérieur; espèces nouvelles et réflexion sur l'étalonnage des échelles continentale et marine. Comptes Rendus de l'Académie des Sciences de Paris Sér. II, 303(8):755-760.

Aguilar, J. P., M. Calvet, and J. Michaux. 1994. Les rongeurs de Castelnou 6 (Pyrénées-orientales, France) et les corrélations entre faunes ibériques et françaises au Miocène moyen. N. Jb. Geol. Paläont. Abh., 192(1):109-131.

Aguilar, J., G. Clauzon, and J. Michaux. 1999. Nouveaux Cricétidés (Rodentia, Mammalia) dans le Miocène moyen de la région de Digne (Alpes de Haute Provence) Systématique, Biocronologie, Corrélations. Paleontographica, 253(1-3):1-28.

Agustí, J., L. Cabrera & S. Moyá-Solá. 1985. Sinopsis estratigráfica del Neógeno de la fosa del Vallès-Penedès. Paleont. i Evol., 18:57-81.

Alberdi, M. T., E. Jiménez, J. Morales, and C. Sesé. 1981. Moratines: primeros micromamíferos en el Mioceno medio del área de Madrid. Estudios Geológicos, 37:291-305.

Alcalá, L., A. Alonso-Zarza, M. Álvarez-Sierra, B. Azanza, J. Calvo, J. Cañaveras, J. v. Dam, M. Garcés, W. Krijgsman, A. v. d. Meulen, P. Pélaez-Campomanes, Pérez-González.A, S. Sánchez Moral, R. Sancho, and E. Sanz Rubio. 2000. El registro sedimentario y faunístico de las cuencas de calatayud-daroca y teruel. evolución paleoambiental y paleoclimática durante el neógeno. Revista de la Sociedad Geológica de España 13:323-343.

Álvarez Sierra, M. A., I. García Paredes, and P. Peláez-Campomanes. 2006. Middle Miocene Rodents from the Tarazona Area. Beiträge zur Paläontologie 30:5-13.

Antunes, M., and P. Mein. 1977. Contributions à la paléontologie du miocène moyen continental du bassin du Tage. III. Mammifères-póvoa de Santarem, pero filho et choes (Secorio) conclusiones generales. Ciéncias da Terra (UNL), 2:143-165.

Bowdich, T. E. 1821. An Analysis of the Natural Classification of Mamalia for the Use of Students and Travellers. 115 pp. Smith, J., Paris.

Bulot, C. 1980. Nouvelle description de deux especes du genre *Megacricetodon* (Cricetidae, Rodentia) du Miocene de Bezian (Zone de La Romieu). Bulletin du Museum National d'Histoire Naturelle Section C Sciences de la Terre Paleontologie Geologie Mineralogie, 2(1):3-16.

Daams, R., L. Alcalá, M. A. Alvarez Sierra, B. Azanza, J. A. van Dam, A. J. van der Meulen, J. Morales, M. Nieto, P. Peláez-Campomanes, and D. Soria. 1998. A stratigraphical framework for Miocene (MN4-MN13) continental sediments of central Spain. Comptes Rendus de l'Academie des Sciences, Serie II. Sciences de la Terre et des Planetes 327:625-631.

Daams, R., and M. Freudenthal. 1988a. Cricetidae (Rodentia) from the type-Aragonian; the genus *Megacricetodon*; pp. 39-132 *in* M. Freudenthal (ed.), Biostratigraphy and paleoecology of the Neogene micromammalian faunas from the Calatayud-Teruel Basin (Spain). Scripta Geologica, Special Issue 1, Leiden.

Daams, R., and M. Freudenthal. 1988b. Synopsis of the Dutch-Spanish collaboration program in the Neogene of the Calatayud-Teruel basin; pp. 3-18 *in* M. Freudenthal (ed.), Biostratigraphy and paleoecology of the Neogene micromammalian faunas from the Calatayud-Teruel Basin (Spain). Scripta Geologica, Special Issue 1, Leiden.

Daams, R., M. Freudenthal, and M. Alvarez-Sierra. 1987. Ramblian: a new stage for continental deposits of early Miocene age. Geologie en Minjbouw 65:297-308.

Daams, R., A. J. van der Meulen, M. A. Álvarez-Sierra, P. Peláez-Campomanes, J. P. Calvo, M. A. Alonso Zarza, and W. Krijgsman. 1999. Stratigraphy and sedimentology of the Aragonian (Early to Middle Miocene) in its type area (North-Central Spain). Newsletters on Stratigraphy 37:103-139.

Fahlbusch, V. 1964. Die Cricetiden (Mam.) der Oberen Süsswasser-Molasse Bayerns. Bayerische Akademie Wissenschaften. Mathematisch-naturwissenschaftliche Klasse. Munchen 118:1-135.

Freudenthal, M. 1963. Entwicklungsstufen der Miozänen Cricetodontinae (Mam. Rod.). In *Mittelspaniens und ihre Stratigraphische Bedeutung*, pp. 107. Ricks University, Utrecht.

García-Moreno, E. 1987. El género *Megacricetodon* (Cricetidae, Rod.) en el Aragoniense y Vallesiense de la Cuenca del Duero. Relaciones filogeneticas. Col-Pa 41:51-106.

Hernández-Ballarín, V., A. Oliver, and P. Pelaez-Campomanes. 2011. Revisión de las asociaciones de mamíferos del tránsito Aragoniense medio y superior de la Cuenca de Madrid; pp. 173-182 *in* A. Pérez-García, F. Gascó, J. M. Gasulla, and F. Escaso (eds.), Viajando a Mundos Pretéritos. Ayuntamiento de Morella, Morella (Castellón).

Hernández Fernández, M., J. A. Cárdaba, J. Cuevas-González, O. Fesharaki, M. J. Salesa, B. Corrales, L. Domingo, J. Elez, P. López Guerrero, N. Sala-Burgos, J. Morales, and N. López Martínez. 2006. Los yacimientos de vertebrados del Mioceno medio de Somosaguas (Pozuelo de Alarcón, Madrid): implicaciones paleoambientales y paleoclimáticas. Estudios Geológicos 62:263-294.

Herráez, E. 1993. Micromamiferos (Roedores y Lagomorfos) del Mioceno del área de Madrid: Estudio sistemático y bioestratigráfico, Universidad Complutense, Madrid, 338 pp.

Illiger, J. K. W. 1811. Überblick der Säugthiere nach ihrer Vertheilung über die Welttheile.; pp. 39-160 *in* W. d. Gruyter (ed.), Abhandlungen de physikalischen Klasse der Königlich-Preussischen Akademie der Wissenschaften. Realschul-Buchhandlung, Berlin.

Kälin, D., and B. Engesser. 2001. Die Jungmiozäne Säugetierfauna vom Nebelbergweg bei Nunningen (Kanton Solothurn, Schweiz). Schweizerische Paläontologische Abhandlungen, 121:1-61.

Lazzari, V., and J. P. Aguilar. 2007. Les *Megacricetodon* du gisement karstique miocène moyen de Blanquatère 1 (Pyrénées-Orientales, Sud de la France): nouvelles espèces, implications biochronologique et phylogénetique. Geobios, 40: 91-111.

López Martínez, N., C. Sesé Benito, and E. Herráez Igualador. 1983. Los yacimientos de Micromamíferos del área de Madrid. Informe para el proyecto Geología de Madrid. Excmo. Ayuntamiento. Excma. Diputación. Instituto Geológico y Minero de España y Fac. de Ciencias Geológicas de la Universidad Complutense de Madrid.

López-Martínez, N., C. Sesé Benito, and E. Herráez 1987. Los yacimientos de Micromamíferos del área de Madrid. Boletín Geológico y Minero, XCVIII-II: 159-176.

Lopez Olmedo, F., J. A. Diaz de Neira, A. Martin Serrano, J. P. Calvo Sorando, J. Morales Romero, and P. Pelaez-Campomanes. 2004. Unidades estratigraficas en el registro sedimentario neogeno del sector occidental de la cuenca de Madrid, Vol. 17 (1-2), pp. 87-101. Sociedad Geologica de España.

Mein, P. 1958. Les mammifères de la faune sidérolithique du Vieux -Collonges. Nouvelles Archives du Muséum d'Histoire Naturelle de Lyon 5:1-122.

Murelaga, X., F. J. Perez-Rivares, M. Vazquez-Urbez, and M. C. Zuluaga. 2008. New biostratigraphic and paleoecologic data from the middle Miocene (Aragonian) from the Tarazona de Aragon area (Ebro Basin) Zaragoza Province, Spain. Ameghiniana 45.

Oliver, A. and P. Peláez-Campomanes. 2013. *Megacricetodon vandermeuleni*, sp. nov. (Rodentia, Mammalia), from the Spanish Miocene: a new evolutionary framework for *Megacricetodon*. Journal of Vertebrate Paleontology, 33(4):943-955.

Peláez-Campomanes, P., and R. Daams. 2002. Middle Miocene rodents from Pasalar, Anatolia, Turkey. Acta Palaeontologica Polonica, 47(1):125-132.

Ruiz-Sánchez, F. J., C. D. Santisteban, and J. I. Lacomba. 2005. Cazuma 1, nueva localidad de micromamíferos (Mammalia, Rodentia) del Aragoniense superior en la cuenca de Quesa-Bicorp (prov. Valencia). Revista Española de Paleontología(extraordinario X. XIX Jornadas de Paleontología):101-109.

Schaub, S. 1925. Die Hamsterartige Nagetiere des Tertiärs und ihre lebenden Verwandten. Abhandlungen des Schweizerischen paläontologische Gesellschaft - Mémoires de la Société paléontologique suisse 45 (Années1921-25):1-114.

Schaub, S. 1944. Cricetodontiden der Spanischen Halbinsel. Eclogae Geologicae Helvetiae. Lausanne, 37(2):453-457.

Sesé, C. and C. Jiménez Rodrigo. 2014. El Aragoniense Medio y Superior en el Suroeste de Madrid: Los nuevos yacimientos de Micromamíferos del Mioceno Medio de Villaviciosa de Odón y Leganés. Estudios Geológicos, 70(1):1-25.

Sesé, C., N. López Martínez, and E. Herráez. 1985. Micromamíferos (Insectívoros, Roedores y Lagomorfos) de la provincia de Madrid, p. 29-39. *In* M. T. Alberdi (ed.), Geología y Paleontología del Terciario continental de la provincia de Madrid. Museo Nacional de Ciencias Naturales - CSIC, Madrid.

APPENDIX 7.1

DISTRIBUTION OF CHARACTER STATES

Table 1. Division of the anterocone M1

Localities					N	MV
Nombrevilla 1			14	(100%)	14	2,00
Carrilanga 1			19	(100%)	19	2,00
Solera	1	(0,4%)	258	(99,6%)	259	2,00
Toril 1			105	(100%)	105	2,00
Las Planas 5H			46	(100%)	46	2,00
Alcocer 2	2	(8%)	23	(92%)	25	1,92
Villafeliche 9			87	(100%)	87	2,00
Las Planas 5K			14	(100%)	14	2,00
Las Planas 5L			16	(100%)	16	2,00
Arroyo del Val 6	5	(100%)			5	1,00
Borjas	1	(1%)	110	(99%)	111	1,99
Manchones			230	(100%)	230	2,00
Valalto 1B	1	(8%)	11	(92%)	12	1,92
Las Planas 5B	1	(1%)	69	(99%)	70	1,99
Las Umbrias 22			8	(100%)	8	2,00
Las Umbrias 20			1	(100%)	1	2,00
Las Umbrias 18			1	(100%)	1	2,00

Table 2. Anterior cingulum M1

Localities							N	MV
Nombrevilla 1					14	(100%)	14	3,00
Carrilanga 1	3	(16%)			16	(84%)	19	2,68
Solera	33	(13%)			226	(87%)	259	2,75
Toril 1	16	(15%)			89	(85%)	105	2,70
Las Planas 5H	3	(7%)			43	(93%)	46	2,87
Alcocer 2	2	(8%)			23	(92%)	25	2,84
Villafeliche 9	3	(3%)			84	(97%)	87	2,93
Las Planas 5K	3	(21%)			11	(79%)	14	2,57
Las Planas 5L					16	(100%)	16	3,00
Arroyo del Val 6			5	(100%)			5	2,00
Borjas	7	(6%)			104	(94%)	111	2,87
Manchones	30	(13%)			200	(87%)	230	2,74
Valalto 1B			9	(75%)	3	(25%)	12	2,25
Las Planas 5B	12	(17%)			58	(83%)	70	2,66
Las Umbrias 22			4	(50%)	4	(50%)	8	2,50
Las Umbrias 20			1	(100%)			1	2,00
Las Umbrias 18					1	(100%)	1	3,00

Table 3. Labial Spur of the Anterolophule M1

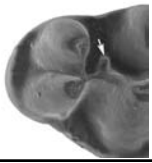
Localities					N
Nombrevilla 1			14	(100%)	14
Carrilanga 1			21	(100%)	21
Solera	12	(5%)	254	(95%)	266
Toril 1	3	(3%)	114	(97%)	117
Las Planas 5H	2	(4%)	52	(96%)	54
Alcocer 2	1	(4%)	27	(96%)	28
Villafeliche 9	4	(4%)	100	(96%)	104
Las Planas 5K	1	(7%)	14	(93%)	15
Las Planas 5L	1	(6%)	15	(94%)	16
Arroyo del Val 6			5	(100%)	5
Borjas	12	(10%)	106	(90%)	118
Manchones	10	(4%)	225	(96%)	235
Valalto 1B	2	(18%)	9	(82%)	11
Las Planas 5B	10	(14%)	64	(86%)	74
Las Umbrias 22			11	(100%)	11
Las Umbrias 20			1	(100%)	1
Las Umbrias 18			1	(100%)	1

Table 4. Protolophule of the M1

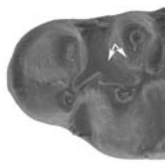
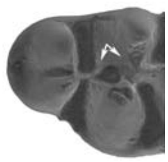
Localities							N
Arroyo del Val 6	5	(100%)					5
Valalto 1B	10	(91%)			1	(9%)	11
Las Umbrias 22	12	(100%)					12
Las Umbrias 20	1	(100%)					1
Las Umbrias 18	1	(100%)					1

Table 5. Ectoloph M1

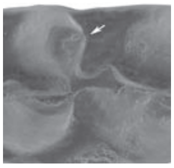
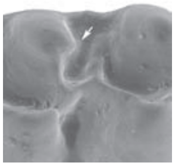
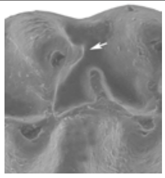
Localities							N	MV
Nombrevilla 1			1	(6%)	15	(94%)	16	2,94
Carrilanga 1	8	(42%)	11	(58%)			19	1,58
Solera	28	(11%)	96	(39%)	120	(49%)	244	2,38
Toril 1	23	(20%)	61	(53%)	31	(27%)	115	2,07
Las Planas 5H	4	(8%)	24	(47%)	23	(45%)	51	2,37
Alcocer 2	6	(17%)	15	(42%)	15	(42%)	36	2,25
Villafeliche 9	9	(8%)	52	(49%)	45	(42%)	106	2,34
Las Planas 5K	1	(6%)	4	(25%)	11	(69%)	16	2,63
Las Planas 5L	1	(6%)	6	(38%)	9	(56%)	16	2,50
Arroyo del Val 6	2	(40%)	1	(20%)	2	(40%)	5	2,00
Borjas	16	(14%)	70	(59%)	32	(27%)	118	2,14
Manchones	32	(14%)	112	(50%)	81	(36%)	225	2,22
Valalto 1B	2	(18%)	5	(45%)	4	(36%)	11	2,18
Las Planas 5B	15	(20%)	30	(41%)	29	(39%)	74	2,19
Las Umbrias 22	1	(8%)	7	(58%)	4	(33%)	12	2,25
Las Umbrias 20					1	(100%)	1	3,00
Las Umbrias 18					1	(100%)	1	3,00

Table 6. Mesoloph M1

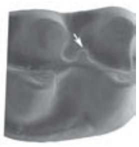
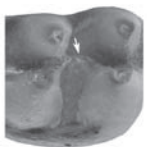
Localities									N	MV
Nombrevilla 1					1	(6%)	15	(94%)	16	3,94
Carrilanga 1			1	(5%)	4	(19%)	16	(76%)	21	3,71
Solera			21	(9%)	41	(17%)	177	(74%)	239	3,65
Toril 1	1	(1%)	18	(17%)	33	(30%)	57	(52%)	109	3,34
Las Planas 5H	1	(2%)	14	(27%)	7	(13%)	30	(58%)	52	3,27
Alcocer 2	2	(5%)	24	(63%)	8	(21%)	4	(11%)	38	2,37
Villafeliche 9	3	(3%)	25	(23%)	33	(30%)	49	(45%)	110	3,16
Las Planas 5K	1	(7%)	6	(40%)	4	(27%)	4	(27%)	15	2,73
Las Planas 5L			5	(31%)	7	(44%)	4	(25%)	16	2,94
Arroyo del Val 6					3	(60%)	2	(40%)	5	3,40
Borjas	2	(2%)	30	(24%)	43	(34%)	50	(40%)	125	3,13
Manchones	8	(3%)	66	(26%)	61	(24%)	115	(46%)	250	3,13
Valalto 1B	1	(9%)	1	(9%)	9	(82%)			11	2,73
Las Planas 5B	10	(14%)	34	(47%)	18	(25%)	11	(15%)	73	2,41
Las Umbrias 22					11	(92%)	1	(8%)	12	3,08
Las Umbrias 20					1	(100%)			1	3,00
Las Umbrias 18					1	(100%)			1	3,00

Table 7. Connection Mesoloph-Ectoloph M1

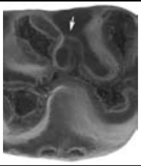
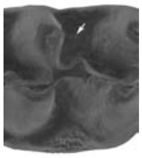
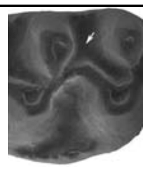
Localities									N
Nombrevilla 1			1	(6%)			15	(94%)	16
Carrilanga 1			5	(24%)			16	(76%)	21
Solera	15	(6%)	47	(20%)			177	(74%)	239
Toril 1	7	(6%)	45	(41%)			57	(52%)	109
Las Planas 5H	4	(8%)	18	(35%)			30	(58%)	52
Alcocer 2	4	(11%)	30	(79%)			4	(11%)	38
Villafeliche 9	3	(3%)	58	(53%)			49	(45%)	110
Las Planas 5K	7	(47%)	4	(27%)			4	(27%)	15
Las Planas 5L			12	(75%)			4	(25%)	16
Arroyo del Val 6			3	(60%)	1	(20%)	1	(20%)	5
Borjas	9	(7%)	66	(53%)			50	(40%)	125
Manchones	23	(9%)	112	(45%)			115	(46%)	250
Valalto 1B	1	(9%)	7	(64%)	2	(18%)	1	(9%)	11
Las Planas 5B	17	(23%)	45	(62%)			11	(15%)	73
Las Umbrias 22			10	(83%)	1	(8%)	1	(8%)	12
Las Umbrias 20			1	(100%)					1
Las Umbrias 18			1	(100%)					1

Table 8. Entomesoloph M1

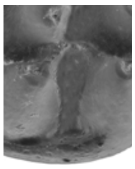
Localities			N
Arroyo del Val 6	5	(100%)	5
Valalto 1B	11	(100%)	11
Las Umbrias 22	13	(100%)	13
Las Umbrias 20	1	(100%)	1
Las Umbrias 18	1	(100%)	1

Table 9. Metalophule M1

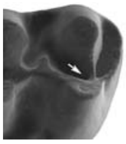
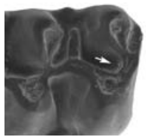
Localities									N
Nombrevilla 1					2	(14%)	12	(86%)	14
Carrilanga 1					11	(52%)	10	(48%)	21
Solera			10	(5%)	150	(70%)	53	(25%)	213
Toril 1	4	(5%)	12	(16%)	51	(69%)	7	(9%)	74
Las Planas 5H	1	(2%)	8	(16%)	34	(67%)	8	(16%)	51
Alcocer 2			11	(34%)	20	(63%)	1	(3%)	32
Villafeliche 9			9	(10%)	58	(64%)	23	(26%)	90
Las Planas 5K	3	(21%)	8	(57%)	3	(21%)			14
Las Planas 5L			10	(67%)	3	(20%)	2	(13%)	15
Arroyo del Val 6					3	(75%)	1	(25%)	4
Borjas	1	(1%)	55	(50%)	48	(43%)	7	(6%)	111
Manchones	5	(2%)	75	(33%)	131	(57%)	19	(8%)	230
Valalto 1B	1	(9%)			9	(82%)	1	(9%)	11
Las Planas 5B	2	(3%)	45	(67%)	19	(28%)	1	(1%)	67
Las Umbrias 22			1	(12,5%)	6	(75%)	1	(12,5%)	8
Las Umbrias 20					1	(100%)			1
Las Umbrias 18					1	(100%)			1

Table 10. Protolophule M2

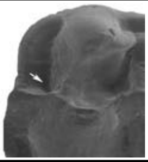
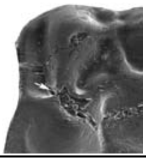
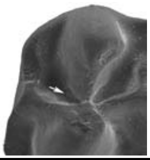
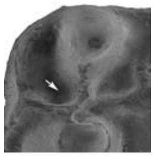
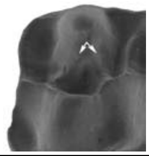
Localities											N
Nombrevilla 1	1	(6%)			10	(63%)	5	(31%)			16
Carrilanga 1			1	(9%)	10	(91%)					11
Solera	23	(21%)	43	(40%)	25	(23%)	15	(14%)	2	(2%)	108
Toril 1	26	(26%)	45	(45%)	8	(8%)	13	(13%)	8	(8%)	100
Las Planas 5H	10	(28%)	5	(14%)	10	(28%)	8	(22%)	3	(8%)	36
Alcocer 2	7	(35%)	2	(10%)	5	(25%)	6	(30%)			20
Villafeliche 9	22	(24%)	37	(41%)	15	(17%)	14	(16%)	2	(2%)	90
Las Planas 5K	10	(43%)	7	(30%)	4	(17%)			2	(9%)	23
Las Planas 5L	8	(42%)	2	(11%)	4	(21%)	5	(26%)			19
Arroyo del Val 6	2	(50%)	1	(25%)			1	(25%)			4
Borjas	43	(34%)	51	(40%)	10	(8%)	15	(12%)	7	(6%)	126
Manchones	61	(36%)	37	(22%)	27	(16%)	29	(17%)	14	(8%)	168
Valalto 1B	4	(40%)	3	(30%)	1	(10%)	2	(20%)			10
Las Planas 5B	44	(54%)	19	(23%)	7	(9%)	6	(7%)	6	(7%)	82
Las Umbrias 22	2	(13%)	1	(6%)	2	(13%)	5	(31%)	6	(38%)	16
Las Umbrias 20									1	(100%)	1

Table 11. Protolophule M2 bis

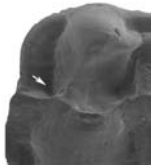
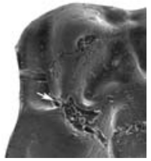
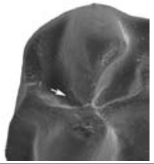
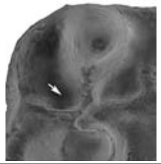
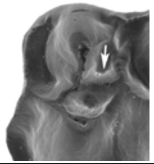
Localities													N
Nombrevilla 1	1	(6%)			10	(63%)	5	(31%)					16
Carrilanga 1			1	(9%)	10	(91%)							11
Solera	23	(21%)	43	(40%)	25	(23%)	15	(14%)	2	(2%)			108
Toril 1	26	(26%)	45	(45%)	8	(8%)	13	(13%)	8	(8%)			100
Las Planas 5H	10	(28%)	5	(14%)	10	(28%)	8	(22%)	3	(8%)			36
Alcocer 2	7	(35%)	2	(10%)	5	(25%)	6	(30%)					20
Villafeliche 9	22	(24%)	37	(41%)	15	(17%)	14	(16%)	2	(2%)			90
Las Planas 5K	10	(43%)	7	(30%)	4	(17%)			2	(9%)			23
Las Planas 5L	8	(42%)	2	(11%)	4	(21%)	5	(26%)					19
Arroyo del Val 6	2	(50%)	1	(25%)			1	(25%)					4
Borjas	43	(34%)	51	(40%)	10	(8%)	15	(12%)	7	(6%)			126
Manchones	61	(36%)	37	(22%)	27	(16%)	29	(17%)	14	(8%)			168
Valalto 1B	4	(40%)	3	(30%)	1	(10%)	2	(20%)					10
Las Planas 5B	44	(54%)	19	(23%)	7	(9%)	6	(7%)	6	(7%)			82
Las Umbrias 22	2	(13%)	1	(6%)	2	(13%)	5	(31%)	2	(13%)	4	(25%)	16
Las Umbrias 20									1	(100%)			1

Table 12. Ectoloph M2

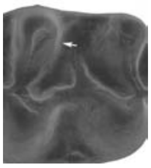
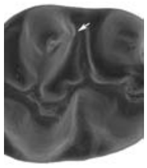
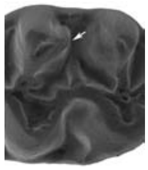
Localities							N	MV
Nombrevilla 1			1	(8%)	11	(92%)	12	2,92
Carrilanga 1	2	(14%)	8	(57%)	4	(29%)	14	2,14
Solera	6	(5%)	54	(42%)	69	(53%)	129	2,49
Toril 1	4	(4%)	36	(32%)	71	(64%)	111	2,60
Las Planas 5H	2	(5%)	7	(18%)	31	(78%)	40	2,73
Alcocer 2	1	(5%)	11	(55%)	8	(40%)	20	2,35
Villafeliche 9	3	(3%)	23	(25%)	65	(71%)	91	2,68
Las Planas 5K	2	(10%)	5	(24%)	14	(67%)	21	2,57
Las Planas 5L	2	(10%)	5	(25%)	13	(65%)	20	2,55
Arroyo del Val 6			2	(40%)	3	(60%)	5	2,60
Borjas			48	(38%)	77	(62%)	125	2,62
Manchones	11	(7%)	52	(33%)	96	(60%)	159	2,53
Valalto 1B			3	(23%)	10	(77%)	13	2,77
Las Planas 5B	8	(9%)	31	(36%)	47	(55%)	86	2,45
Las Umbrias 22			1	(6%)	17	(94%)	18	2,94
Las Umbrias 20					1	(100%)	1	3,00

Table 13. Mesoloph M2

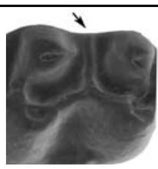
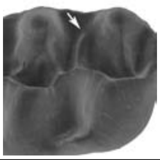
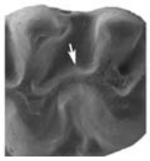
Localities									N
Nombrevilla 1					1	(6%)	15	(94%)	16
Carrilanga 1							13	(100%)	13
Solera	2	(2%)	18	(15%)	26	(21%)	75	(62%)	121
Toril 1	5	(5%)	34	(31%)	26	(23%)	46	(41%)	111
Las Planas 5H	4	(11%)	10	(26%)	4	(11%)	20	(53%)	38
Alcocer 2	1	(5%)	9	(47%)	4	(21%)	5	(26%)	19
Villafeliche 9	2	(2%)	22	(23%)	25	(26%)	46	(48%)	95
Las Planas 5K	3	(11%)	19	(70%)	2	(7%)	3	(11%)	27
Las Planas 5L	3	(15%)	5	(25%)	5	(25%)	7	(35%)	20
Arroyo del Val 6			1	(20%)	4	(80%)			5
Borjas			42	(33%)	29	(23%)	55	(44%)	126
Manchones	3	(2%)	61	(32%)	51	(27%)	76	(40%)	191
Valalto 1B			2	(18%)	8	(73%)	1	(9%)	11
Las Planas 5B	12	(14%)	59	(67%)	6	(7%)	11	(13%)	88
Las Umbrias 22	1	(6%)	1	(6%)	10	(59%)	5	(29%)	17
Las Umbrias 20					1	(100%)			1

Table 14. Connection Mesolph-Ectoloph M2

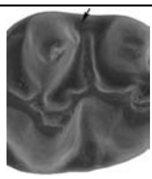
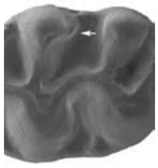
Localities							N
Nombrevilla 1			1	(6%)	15	(94%)	16
Carrilanga 1					13	(100%)	13
Solera	21	(17%)	25	(21%)	75	(62%)	121
Toril 1	29	(26%)	36	(32%)	46	(41%)	111
Las Planas 5H	10	(26%)	8	(21%)	20	(53%)	38
Alcocer 2	6	(32%)	8	(42%)	5	(26%)	19
Villafeliche 9	14	(15%)	35	(37%)	46	(48%)	95
Las Planas 5K	10	(37%)	14	(52%)	3	(11%)	27
Las Planas 5L	4	(20%)	9	(45%)	7	(35%)	20
Arroyo del Val 6			5	(100%)			5
Borjas	26	(20%)	46	(36%)	55	(43%)	127
Manchones	25	(13%)	90	(47%)	76	(40%)	191
Valalto 1B	1	(9%)	9	(82%)	1	(9%)	11
Las Planas 5B	43	(49%)	34	(39%)	11	(13%)	88
Las Umbrias 22	3	(18%)	9	(53%)	5	(29%)	17
Las Umbrias 20			1	(100%)			1

Table 15. Metalophule M2

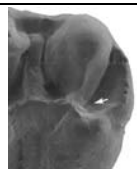
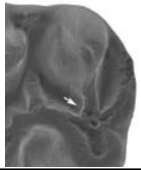
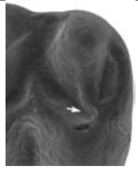
Localities															N
Nombrevilla 1											15	(94%)	1	(6%)	16
Carrilanga 1											10	(100%)			10
Solera			14	(14%)			7	(7%)	4	(4%)	34	(35%)	39	(40%)	98
Toril 1			35	(35%)			14	(14%)	4	(4%)	18	(18%)	28	(28%)	99
Las Planas 5H			9	(27%)			2	(6%)	3	(9%)	13	(39%)	6	(18%)	33
Alcocer 2			5	(28%)			4	(22%)	1	(6%)	5	(28%)	3	(17%)	18
Villafeliche 9			32	(36%)			20	(22%)	6	(7%)	11	(12%)	20	(22%)	89
Las Planas 5K			12	(55%)			3	(14%)	3	(14%)	1	(5%)	3	(14%)	22
Las Planas 5L			9	(47%)			3	(16%)	2	(11%)	2	(11%)	3	(16%)	19
Arroyo del Val 6	1	(20%)	1	(20%)							1	(20%)	2	(40%)	5
Borjas			44	(36%)			18	(15%)	9	(7%)	25	(20%)	26	(21%)	122
Manchones			93	(51%)			18	(10%)	10	(6%)	39	(22%)	21	(12%)	181
Valalto 1B			4	(40%)			2	(20%)	1	(10%)			3	(30%)	10
Las Planas 5B			39	(46%)			21	(25%)	11	(13%)	5	(6%)	8	(10%)	84
Las Umbrias 22			6	(38%)	1	(6%)	1	(6%)	2	(13%)	4	(25%)	2	(13%)	16
Las Umbrias 20									1	(100%)					1

Table 16. Anteroconid m1

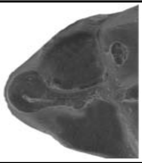
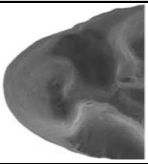
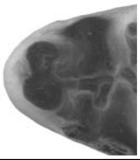
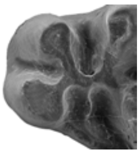
Localities									N	MV
Nombrevilla 1							17	(100%)	17	4,00
Carrilanga 1					1	(5%)	20	(95%)	21	3,95
Solera			1	(1%)	32	(20%)	128	(80%)	161	3,79
Toril 1	6	(5%)	16	(13%)	37	(30%)	63	(52%)	122	3,29
Las Planas 5H	1	(2%)	1	(2%)	7	(17%)	33	(79%)	42	3,71
Alcocer 2			1	(4%)	15	(63%)	8	(33%)	24	3,29
Villafeliche 9	2	(2%)	11	(12%)	45	(47%)	37	(39%)	95	3,23
Las Planas 5K			4	(50%)	3	(38%)	1	(13%)	8	2,63
Las Planas 5L			7	(25%)	20	(71%)	1	(4%)	28	2,79
Arroyo del Val 6	2	(40%)	1	(20%)	1	(20%)	1	(20%)	5	2,20
Borjas	5	(4%)	28	(25%)	67	(60%)	12	(11%)	112	2,77
Manchones	44	(19%)	59	(26%)	78	(34%)	48	(21%)	229	2,57
Valalto 1B	4	(44%)	4	(44%)	1	(11%)			9	1,67
Las Planas 5B	25	(32%)	42	(55%)	10	(13%)			77	1,81
Las Umbrias 22	5	(63%)	2	(25%)	1	(13%)			8	1,50
Las Umbrias 19			1	(100%)					1	2,00

Table 17. Metalophulid m1

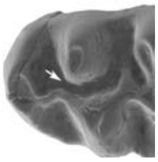
Localities					N
Arroyo del Val 6			5	(100%)	5
Valalto 1B	1	(11%)	8	(89%)	9
Las Umbrias 22			14	(100%)	14
Las Umbrias 19			1	(100%)	1

Table 18. Mesolophid m1

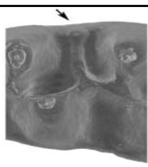
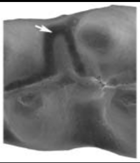
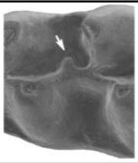
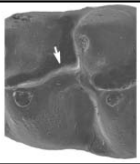
Localities									N	MV
Nombrevilla 1							18	(100%)	18	4,00
Carrilanga 1			1	(4%)			24	(96%)	25	3,92
Solera			6	(3%)	34	(18%)	145	(78%)	185	3,75
Toril 1			2	(1%)	21	(13%)	136	(86%)	159	3,84
Las Planas 5H	1	(2%)			7	(13%)	45	(85%)	53	3,81
Alcocer 2	1	(3%)	1	(3%)	8	(23%)	25	(71%)	35	3,63
Villafeliche 9			2	(2%)	30	(25%)	87	(73%)	119	3,71
Las Planas 5K			1	(8%)	4	(33%)	7	(58%)	12	3,50
Las Planas 5L					15	(48%)	16	(52%)	31	3,52
Arroyo del Val 6					2	(40%)	3	(60%)	5	3,60
Borjas			6	(4%)	31	(22%)	101	(73%)	138	3,69
Manchones	1	(1%)	11	(4%)	50	(19%)	196	(76%)	258	3,71
Valalto 1B					5	(56%)	4	(44%)	9	3,44
Las Planas 5B	3	(3%)	7	(7%)	31	(33%)	54	(57%)	95	3,43
Las Umbrias 22					3	(23%)	10	(77%)	13	3,77
Las Umbrias 19					1	(100%)			1	3,00

Table 19. Lingual Anterolophid m2

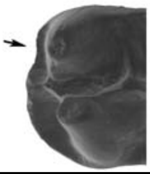
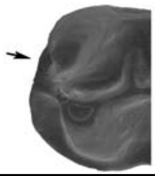
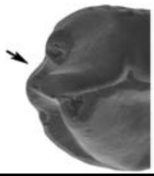
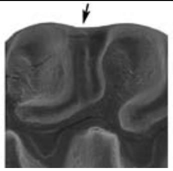
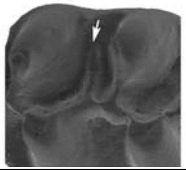
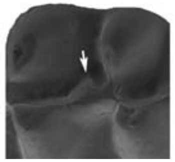
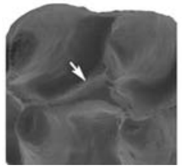
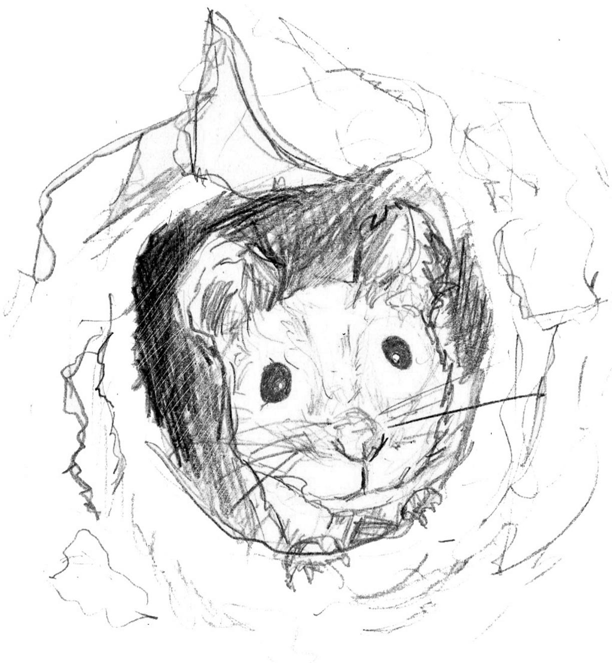
Localities							N	MV
Nombrevilla 1					18	(100%)	18	3,00
Carrilanga 1			4	(19%)	17	(81%)	21	2,81
Solera			71	(40%)	108	(60%)	179	2,60
Toril 1	2	(2%)	52	(40%)	76	(58%)	130	2,57
Las Planas 5H			7	(20%)	28	(80%)	35	2,80
Alcocer 2			3	(13%)	21	(88%)	24	2,88
Villafeliche 9	1	(1%)	31	(27%)	84	(72%)	116	2,72
Las Planas 5K			10	(50%)	10	(50%)	20	2,50
Las Planas 5L			14	(58%)	10	(42%)	24	2,42
Arroyo del Val 6			3	(100%)			3	2,00
Borjas	2	(2%)	42	(36%)	73	(62%)	117	2,61
Manchones	7	(3%)	147	(65%)	72	(32%)	226	2,29
Valalto 1B	1	(14%)	6	(86%)			7	1,86
Las Planas 5B			34	(42%)	47	(58%)	81	2,58

Table 20. Mesolophid m2

Localities									N	MV
Nombrevilla 1							14	(100%)	14	4,00
Carrilanga 1							20	(100%)	20	4,00
Solera			10	(5%)	66	(33%)	123	(62%)	199	3,57
Toril 1	1	(1%)	10	(6%)	66	(43%)	77	(50%)	154	3,42
Las Planas 5H			1	(2%)	15	(35%)	27	(63%)	43	3,60
Alcocer 2			4	(14%)	6	(21%)	19	(66%)	29	3,52
Villafeliche 9			5	(4%)	43	(35%)	76	(61%)	124	3,57
Las Planas 5K	1	(4%)	3	(13%)	10	(43%)	9	(39%)	23	3,17
Las Planas 5L			3	(12%)	11	(42%)	12	(46%)	26	3,35
Arroyo del Val 6					3	(60%)	2	(40%)	5	3,40
Borjas	2	(1%)	13	(9%)	48	(33%)	84	(57%)	147	3,46
Manchones	2	(1%)	24	(9%)	81	(31%)	151	(59%)	258	3,48
Valalto 1B			1	(9%)	7	(64%)	3	(27%)	11	3,18
Las Planas 5B	1	(1%)	16	(18%)	41	(46%)	31	(35%)	89	3,15
Las Umbrias 22					6	(38%)	10	(63%)	16	3,63
Las Umbrias 19					1	(100%)			1	3,00

8. Synthesys



8.1. SYNTHESYS

In this chapter we focus on the main bioestratigraphical, paleoecological and paleogeographical results of this work in relation to the *Megacricetodon* species of the Calatayud-Montalbán Basin.

Bioestratigraphical implications

Van der Meulen et al. (2012) in their updating of the Aragonian biostratigraphy, formally defined the local biozones of the early and middle Aragonian in the Calatayud-Montalbán Basin. They defined the biozones from local zone A to local zone E, several of these zones where defined based on the occurrence of *Megacricetodon* or the concurrence of *Megacricetodon* and *Democricetodon*, such as, Zones B, Ca, Da, Db and E.

As had been demonstrated, this genus is very useful as biostratigraphic marker. In fact, the substitution of the different *Megacricetodon* species, could allow us to accurate some of the local zones. Figures 8.1 and 8.2 show the distribution of the different *Megacricetodon* species of the Calatayud-Montalbán Basin through time.

The main bioestratighapical implications of this work are:

1) Local zone Ca is characterize by *Megacricetodon primitivus*. The first occurrence (FO) of *Megacricetodon* in the Iberian Peninsula was in this zone, in the locality of Artesilla (Figure 8.2). This biozone is defined by the concurrence Range zone of *Megacricetodon primitivus* and *Democricetodon decipiens*.

2) Biozone Db is characterized by the co-occurrence of *M. primitivus* with *M. vandermeuleni* (Oliver & Peláez-Campomanes, 2013), which is restricted to this zone. Biozone Db is defined by *M. vandermeuleni* Range zone.

3) According to Van der Meulen et al. (2012), local zone Dc is defined by the interval zone of the FO of *Democricetodon jordensi* and *D. koenigswaldi*. Moreover, this zone contains the FO of *Megacricetodon* n. sp. 2. This new species is *Megacricetodon alvarezae* (see Chapter 5). In addition, based on the size of this *Megacricetodon*, it could be possible to differentiate two zones within this biozone. In the older localities, *M. alvarezae* is larger than the material from the younger sites. This unusual situation occurs both in Calatayud-Montalbán Basin and Madrid Basin (Oliver et al., in preparation).

4) Along local zone Dd occurs the substitution of species of the same lineage; *Megacricetodon collongensis* is restricted to the lower part of the zone, whereas

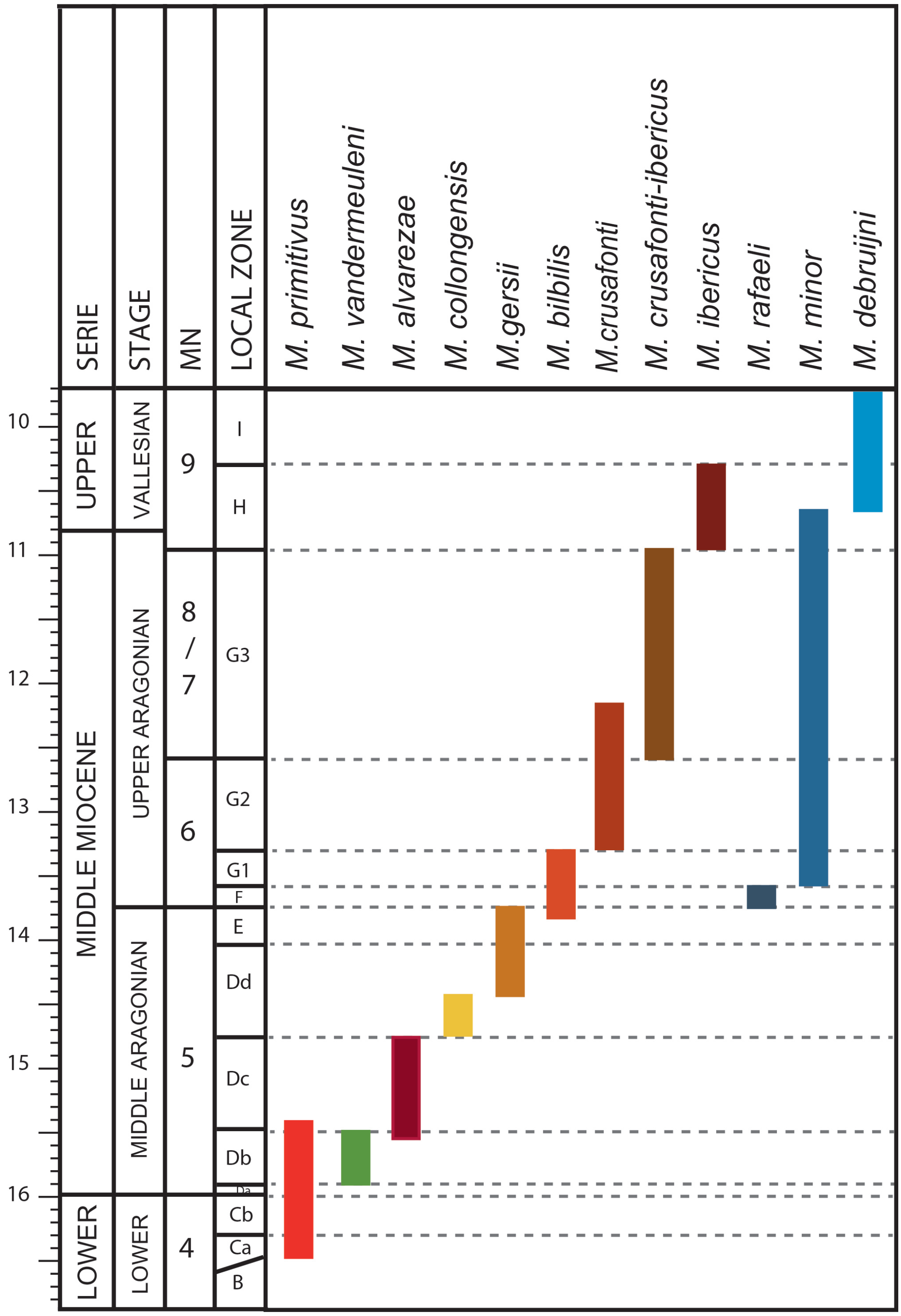


Figure 8.1. Bioestratigraphical distribution of the *Megacricetodon* species from Aragonian and Vallesian of the Calatayud-Montalbán Basin.

M. gersii occurs in the upper part of the zone and disappear in the local zone E (see Chapter 6). The presence of *M. collongensis* in the lower part of the zone (Figures 8.1 and 8.2) is also accompanied by sedimentological differences between lower and upper part of the Dd sediments in the Calatayud-Montalbán Basin. These sedimentological changes, seems to correspond to bioestratigraphic changes within the biozone, which could support a future subdivision of the biozone Dd.

5) *Megacricetodon gersii* is recognized in the local zones Dd and E (middle Aragonian) instead to local zone F (upper Aragonian). This species is used as bioevent to propose biochronological correlation between Spain, Germany and Switzerland (Bolliger, 1997; Kälin, 1997; Kempf et al., 1997; Daams et al., 1999; van Dam et al., 2006; Abdul Aziz et al., 2008; 2010; Kälin & Kempf, 2009; van der Meulen et al., 2011; 2012). Therefore, the first occurrence of *M. gersii* in the Calatayud-Montalbán Basin in the middle part of the local zone Dd predate the first occurrence of this species in Switzerland, contrary to what was previously thought (van der Meulen et al., 2011).

6) According to Daams et al. (1999), local zone F contains two *Megacricetodon* species, *M. gersii* and *M. rafaeli*. The update in the *Megacricetodon* species, allow us to characterize this biozone by the co-occurrence of *Megacricetodon bilbilis* and *M. rafaeli*, the latter one restricted to this biozone. This zone could be defined by the *M. rafaeli* Range zone.

7) Local zone G1 contains two *Megacricetodon* species, *Megacricetodon bilbilis* (instead of *M. gersii* as proposed in Daams et al., 1999) and *M. minor*.

8) Biozone G2 is characterized by the occurrence of *Megacricetodon crusafonti* (Daams et al., 1999; this work).

9) Local zone G3 is characterized by *Megacricetodon minor* and *M. crusafonti-ibericus* (Daams et al., 1999). This zone could be defined as the *Megacricetodon crusafonti-ibericus* Range zone.

10) Biozone H contains *Megacricetodon ibericus* and *M. minor* or *M. debruijni* (Daams et al., 1999). This zone could be defined as the *Megacricetodon ibericus* Range zone.

11) Finally, in local zone I only occurs *Megacricetodon debruijni* (Daams et al., 1999).

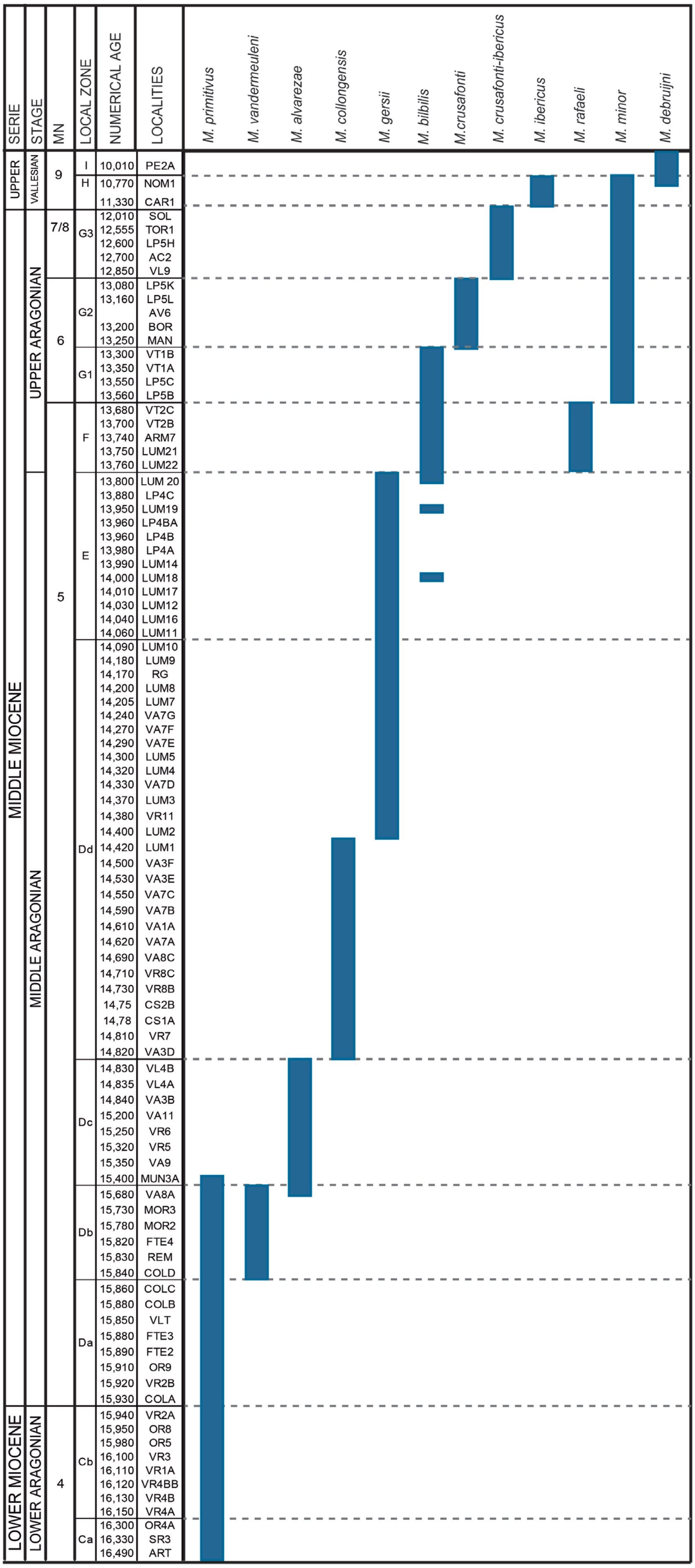


Figure 8.1. Bioestratigraphical distribution of the *Megacricetodon* species from Aragonian and Vallesian of the Calatayud-Montalbán Basin.

Paleoecological implications

Figure 8.1 shows the distribution of the different species since its first occurrence in the lower Aragonian (lower Miocene, MN 4) till its last occurrence in the lower Vallesian (upper Miocene, MN 9). In the lower Aragonian only occurs one *Megacricetodon* species, the small *M. primitivus*, whereas in the lowermost part of the middle Aragonian (local zone Db) coexist two *Megacricetodon* species. The maximum of diversity occurs at the end of biozone Db where coexist three *Megacricetodon* species, two large sized-species (*M. vandermeuleni* and *M. alvarezae*) and the small *M. primitivus*. During the local zone Dc, the diversity decreased very fast from two species at the beginning of the biozone (*M. alvarezae* and the last occurrence of *M. primitivus*) to only one species (*M. alvarezae*) in the rest on the biozone.

Other peak of diversity occurs in the uppermost part of the middle Aragonian and in the upper Aragonian where two *Megacricetodon* species coexist through time but with a faunal replacement between them. In the upper part of the middle Aragonian (upper part of local zone E) coexist two large sized species (*M. gersii* and *M. bilbilis*), whereas in the local zones F, G1, G2, G3 and H occurs a large-sized species (the *M. bilbilis – M. crusafonti – M. crusafonti-ibericus – M. ibericus* lineage) and a small-sized species (*M. rafaeli* and *M. minor*). Finally, in the biozone I only occurs the small *Megacricetodon debruijni*, since in the upper Vallesian the cricetids are replaced by the murids (rats and mice).

The middle Miocene climate changes (Zachos et al., 2001), both the Miocene Climatic Optimum (~16.3-15 Ma) and the Middle Miocene Climate Transition (~15-13.7 Ma) are well correlated with the small mammal succession in the Calatayud-Montalbán Basin (Daams et al., 1988; Daams et al., 1999; van der Meulen et al., 2005; van Dam et al., 2006; Hordijk, 2010; Álvarez-Sierra et al., 2014) and with the Madrid Basin (Peláez-Campomanes et al., 2014).The changes in micromammal record in both basins reflect a high sensitivity to shifts in global climate, in particular in relation to changes in local humidity. The small mammal record is compared with detailed global climate trends from the marine stable isotope record, ODP Site 1146 in the South China Sea (Holbourn et al., 2007) and the Ras il Pellegrin section on Malta (Abels et al., 2005; Mourik, 2010; Mourik et al., 2011); and with the continental precipitation curve (Böhme et al., 2006; 2011).

The different species of *Megacricetodon* are also affected for this variation in the environmental conditions. The main climatic shifts which affected *Megacricetodon* are:

1) The local zone C is interpreted to a warmer environment in relation with biozone B, with major expansion of open vegetation and an increase of aridity. Moreover, there are changes in the community composition with the addition of new arrivals and loss of older lineages (van der Meulen & Daams, 1992; van Dam et al., 2006; Hordijk, 2010). In the Iberian Peninsula, *Megacricetodon* has its first occurrence in this zone.

2) Within the Miocene Climatic Optimum (~15.7-15.5 Ma), the boundary between the local zone Db and Dc coincides with a less favorable environment (drop in humidity and variable temperature), leading to decrease in species richness, equitability and diversity (Peláez-Campomanes et al., 2014). With regard to the *Megacricetodon* species from the Calatayud-Montalbán Basin, both figures (8.1 and 8.2) show in the boundary Db-Dc and increase in the diversity of the species (from two to three species), which is consistent with the drop in equitability.

3) According to Hordijk (2010) the local zones Dd and E comprise a series of immigrations that expand the micromammal community. Within zone Dd (~14.5 Ma), the immigration rate increased, while zone E is marked by the brief disappearance of recent arrivals. The *Megacricetodon* species which occurs in these zones are immigrants from France (*M. collongensis*and *M. gersii*). It is remarkable that the substitution of *M. collongensis*for *M. gersii* was in the same date that these authors proposed. The last occurrence of *M. collongensis*was in Valdemoros 3F (~14.5 Ma) and Las Umbrias 1 (~14.20 Ma), whereas the first occurrence of *M. gersii* was in Las Umbrias 2 (~14.40 Ma) (see Figure 8.2).

4) The Mi3a event (~14.2 Ma), is the first cooling step of the Middle Miocene Climate Transition. This gradual cooling is correlated with the decreasing diversity pattern observed during local zones Dd and E (Álvarez-Sierra et al., 2014; Peláez-Campomanes et al., 2014). However, *Megacricetodon* remains unchanged over this period.

5) The major cooling step in middle Miocene climate (Mi3b event, ~13.8 Ma) represent one of the most variable period in assemblage composition (van der Meulen et al., 2005; van Dam et al., 2006; Hernández-Ballarín et al., 2011). In relation to the *Megacricetodon* species, in this interval takes place the substitution of *M. gersii* for two new species, *M. crusafonti* and *M. rafaeli*.

6) Finally, the Mi4 event, takes places ~13.2-12.8 Ma in the boundary G2-G3. This drop in the temperature is reflected in *Megacricetodon*. The species *M. crusfonti* increase its size and evolves to *M. crusafonti-ibericus*.

Paleogeographical implications

The first occurrence of *Megacricetodon* has been considered by most authors as a single bioevent in Switzerland, Germany and Spain (van der Meulen et al., 2011 and references there), however, according to Oliver & Peláez-Campomanes (2014) and this work, there are at least three main migration events of the genus *Megacricetodon* into Europe during early-middle Miocene, each corresponding to different lineages that probably evolved independently (the Greek lineage, the *M. bavaricus* group and the *M. primitivus* group) See Figure 8.3.

According to Oliver & Peláez-Campomanes (2014) the first wave of *Megacricetodon* in Europe involves the Greek form that occurs in the early Aragonian in the island of Aliveri (Evia island). This form evolved as an endemic Greek form. The small-sized *Megacricetodon hellenicus* evolved through the Komotini area (Karidya I and II), Macedonia (Antonios) and Chios island (Thymiana A and C), during the earliest MN 4 (Oliver & Peláez-Campomanes, 2014).

The *Megacricetodon bavaricus* group is characteristic of the central European basins (Oliver & Peláez-Campomanes, 2013). Supposedly, the earliest representatives of this lineage are from the Czech Republic (*Megacricetodon* from Ořechov and Dolnice 3), in the early MN 4. This form dispersed and evolved through the Central and Southwestern Europe. In Switzerland and Germany, the earliest representatives of this large-sized lineage are *Megacricetodon* aff. *collongensis*, whereas in France is assigned to *Megacricetodon bezianensis*, all of them in the middle MN 4. In the Swiss and German Molasse occur *Megacricetodon* aff. *collongensis* during middle MN 4 (OSM A), evolving in MN 5 to *M. bavaricus* (OSM B), *M.* aff. *bavaricus* (OSM C+D) and finally *M. lappi* (OSM E) (Kälin & Kempf, 2009, Abdul Aziz et al., 2008, 2010). In France, *Megacricetodon bezianensis* keep relatively without variation during MN 4 and MN 5. Finally this group was slowly spreading to the Southwester of Europe. *Megacricetodon vandermeuleni* reached the Iberian Peninsula (Spain) in the middle MN 5 (local zone Db) (Oliver & Peláez-Campomanes 2013).

The third migration event is the migration wave of the *Megacricetodon primitivus* group. The first occurrence of *Megacricetodon primitivus* is in southern France (Gers localities) in the lower part of MN 4, reaching the Iberian Peninsula (Spain and Portugal) in the middle MN 4, local zone Ca (Ginsburg & Bulot, 2000; Oliver & Peláez-Campomanes,

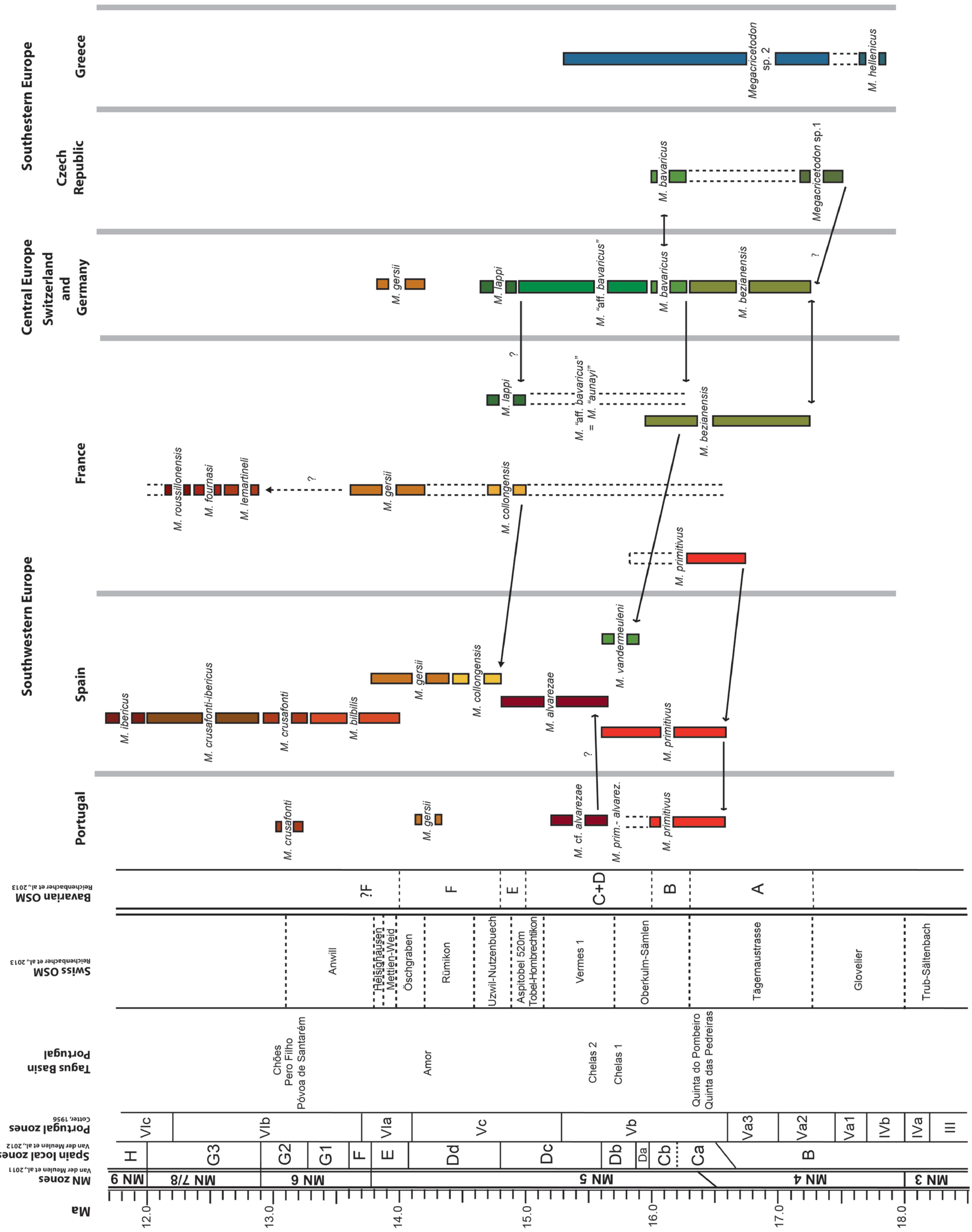


Figure 8.3. Paleogeographic distributions of the migration waves from the different *Megacricetodon* lineages in Europe throughout the Miocene.

in press). In Portugal, during local zone Db (MN 5) occurs an intermediate evolutionary stage of *Megacricetodon* with size of *M. primitivus* but morphology of *M. alvarezae*, which evolves during local zone Dc to a large-sized specie. In Spain, *Megacricetodon alvarezae* enters from Portugal at the end of the local zone Db, dispersing throughout the local zone Dc. In France, *M. primitivus* could be the origin for *M. collongensis* at early MN 5, dispersing to Spain in the lower part of the biozone Dd (middle Aragonian), and evolving to *M. gersii* in the upper part of the local zone Dd. According to Kälin & Kempf (2009), *M. gersii* would have reached Central Europe (Switzerland) in the Oeschgraben zone equivalent to upper part of the Spanish Dd (van der Meulen et al., 2011). Aguilar (1995) suggest that the French *M. gersii* evolves to *M. lemartineli* (locality of Lo Fournas 10), *M. fournasi* (locality of Lo Fournas 10), and finally to *M. roussillonensis* (locality of Lo Fournas 3). These latest forms from MN 7/8 would be endemic from France.

Finally, the *Megacricetodon bilbilis* – *M. ibericus* lineage has been recorded from localities in Southwestern Europe. The first occurrence of this lineage in Spain is *Megacricetodon bilbilis,* during the upper part of local zone E (middle Aragonian). This species remains without variation during biozones F and G1, evolving into *M. crusafonti* in the local zone G2. Representatives of *M. crusafonti* have been recorded from localities in Portugal and France (Aguilar et al., 1994) correlated to the latter zone. The intermediate stage, *M. crusafonti-ibericus*, occurs in local zone G3, which evolves into *M. ibericus* in the early Vallesian (biozone H).

8.2. REFERENCES

Abdul Aziz, H., M. Böhme, A. Rocholl, J. Prieto, J. R. Wijbrans, V. Bachtadse, and A. Ulbig. 2010. Integrated stratigraphy and 40Ar/39Ar chronology of the Early to Middle Miocene Upper Freshwater Molasse in western Bavaria (Germany). International Journal of Earth Sciences 99:1859-1886.

Abdul Aziz, H., M. Böhme, A. Rocholl, A. Zwing, J. Prieto, J. R. Wijbrans, K. Heissig, and V. Bachtadse. 2008. Integrated stratigraphy and 40Ar/39Ar chronology of the Early to Middle Miocene Upper Freshwater Molasse in eastern Bavaria (Germany). International Journal of Earth Sciences 97:115-134.

Abels, H. A., F. J. Hilgen, W. Krijgsman, R. W. Kruk, I. Raffi, E. Turco, and W. J. Zachariasse. 2005. Long-period orbital control on middle Miocene global cooling: Integrated stratigraphy and astronomical tuning of the Blue Clay Formation on Malta. Paleoceanography 20.

Aguilar, J. P. 1995. Evolution de la lignée *Megacricetodon collongensis-Megacricetodon rousillonensis* (Cricetidae, Rodentia, Mammalia) au cours du Miocène inférieur et moyen dans le sud de la France. Palaeovertebrata 24:1-45.

Aguilar, J. P., M. Calvet, and J. Michaux. 1994. Les rongeurs de Castelnou 6 (Pyrénées-orientales, France) et les corrélations entre faunes ibériques et françaises au Miocène moyen. N. Jb. Geol. Paläont. Abh. 192:109-131.

Álvarez-Sierra, M. A., I. García-Paredes, L. W. van den Hoek Ostende, V. Hernández-Ballarín, K. Hordik, P. López-Guerrero, A. Oliver, and P. Peláez-Campomanes. 2014. The Aragonian and Vallesian high-resolution micromammal succession in the Calatayud-Montalbán Basin (Aragón, Spain). 15th RCMNS Interim Colloquium Torino.

Bohme, M., A. Ilg, A. Ossig, and H. Kuchenhoff. 2006. New method to estimate paleoprecipitation using fossil amphibians and reptiles and the middle and late Miocene precipitation gradients in Europe. Geology 34:425-428.

Bohme, M., M. Winklhofer, and A. Ilg. 2011. Miocene precipitation in Europe: Temporal trends and spatial gradients. Palaeogeography Palaeoclimatology Palaeoecology 304:212-218.

Bolliger, T. v. 1997: The current knowledge of the biozonation with small mammals in the upper freshwater molasse in Switzerland, especially the Hörnli-fan. Paper presented at the BiochroM>97, Montpellier, 1997.

Daams, R., and M. Freudenthal. 1988. Cricetidae (Rodentia) from the type-Aragonian; the genus *Megacricetodon*; pp. 39-132 *in* M. Freudenthal (ed.), Biostratigraphy and paleoecology of the Neogene micromammalian faunas from the Calatayud-Teruel Basin (Spain). Scripta Geologica, Special Issue 1, Leiden.

Daams, R., A. J. van der Meulen, M. A. Álvarez-Sierra, P. Peláez-Campomanes, and W. Krijgsman. 1999. Aragonian stratigraphy reconsidered, and a re-evaluation of the middle Miocene mammal biochronology in Europe. Earth and Planetary Science Letters 165:287-294.

Ginsburg, L., and C. Bulot. 2000. Le cadre stratigraphique du site de Sansan. Memoires du Museum National d'Histoire Naturelle 183:39-67.

Hernández-Ballarín, V., A. Oliver, and P. Pelaez-Campomanes. 2011. Revisión de las asociaciones de mamíferos del tránsito Aragoniense medio y superior de la Cuenca de Madrid; pp. 173-182 *in* A. Pérez-García, F. Gascó, J. M. Gasulla, and F. Escaso (eds.), Viajando a Mundos Pretéritos. Ayuntamiento de Morella, Morella (Castellón).

Holbourn, A., W. Kuhnt, M. Schulz, F. J.A., and N. Andersen. 2007. Orbitally-paced climate evolution during the middle Miocene «Monterey» carbon-isotope excursion. Earth and Planetary Science Letters 261:534-550.

Hordijk, K. 2010. Perseverance of pikas in the Miocene: In *Faculty of Geosciences*, pp. 232. Utrecht University, Utrecht.

Kälin, D. 1997: The mammal zonation of the Upper Marine Molasse of Switzerland reconsidered. A local biozonation of MN2-MN5. Paper presented at the Actes du Congrès BiochromM'97, Mémoires et Travaux de l'E.P.H.E., Institut de Montpellier, 1997.

Kälin, D., and O. Kempf. 2009. High-resolution stratigraphy from the continental record of the Middle Miocene Northern Alpine Foreland Basin of Switzerland. Neues Jahrbuch Fur Geologie Und Palaontologie-Abhandlungen 254:177-235.

Mourik, A. A., H. A. Abels, F. J. Hilgen, A. Di Stefano, and W. J. Zachariasse. 2011. Improved astronomical age constraints for the middle Miocene climate transition based on high-resolution stable isotope records from the central Mediterranean Maltese Islands. Paleoceanography 26.

Mourik, A. A., J. F. Bijkerk, A. Cascella, S. K. Husing, F. J. Hilgen, L. J. Lourens, and E. Turco. 2010. Astronomical tuning of the La Vedova High Cliff section (Ancona, Italy)-Implications of the Middle Miocene Climate Transition for Mediterranean sapropel formation. Earth and Planetary Science Letters 297:249-261.

Oliver, A., and P. Pelaez-Campomanes. 2013. *Megacricetodon vandermeuleni*, sp. nov. (Rodentia, Mammalia), from the Spanish Miocene: a new evolutionary framework for *Megacricetodon*. Journal of Vertebrate Paleontology 33:943-955.

Oliver, A., and P. Pelaez-Campomanes. 2014. Early Miocene evolution of the genus *Megacricetodon* in Europe and its palaeobiogeographical implications. Acta Palaeontologica Polonica. doi:http://dx.doi.org/10.4202/app.00099.2014.

Oliver, A., and P. Peláez-Campomanes. In press. Evolutionary patterns of early and middle Aragonian (Miocene) of *Megacricetodon* (Rodentia, Mammalia) from Spain. Palaeontographica Abteilung A.

Oliver, A., V. Hernández-Ballarín, and P. Peláez-Campomanes. In preparation. New insigtht of the *Megacricetodon* from the middle Aragonian (middle Miocene) of the Iberian Peninsula: A new species with implications in bioestratigraphy.

Peláez-Campomanes, P., V. Hernández-Ballarín, and A. Oliver. 2014. The rodent fossil record from the Miocene of the Madrid Basin (Spain): An example of climatically driven community evolutionary patterns. SVP, Berlin: 202-203.

van Dam, J. A., H. A. Aziz, M. A. Álvarez Sierra, F. J. Hilgen, L. W. V. D. H. Ostende, L. J. Lourens, P. Mein, A. J. van der Meulen, and P. Pelaez-Campomanes. 2006. Long-period astronomical forcing of mammal turnover. Nature 443:687-691.

van der Meulen, A. J., and R. Daams. 1992. Evolution of Early-Middle Miocene rodent faunas in relation to long-term palaeoenvironment changes. Palaeogeography, Palaeoclimatology, Palaeoecology 93:227-253.

van der Meulen, A. J., I. Garcia-Paredes, M. A. Alvarez-Sierra, L. W. V. Ostende, K. Hordijk, A. Oliver, P. Lopez-Guerrero, V. Hernandez-Ballarin, and P. Pelaez-Campomanes. 2011. Biostratigraphy or biochronology? Lessons from the Early and Middle Miocene small Mammal Events in Europe. Geobios 44:309-321.

van der Meulen, A. J., I. García-Paredes, M. A. Álvarez-Sierra, L. W. van den Hoek Ostende, K. Hordijk, A. Oliver, and P. Peláez-Campomanes. 2012. Updated Aragonian biostratigraphy: Small Mammal distribution and its implications for the Miocene European Chronology. Geologica Acta 10:159-179.

van der Meulen, A. J., P. Peláez-Campomanes, and S. A. Levin. 2005. Age structure, residents, and transients of Miocene rodent communities. American Naturalist 165:108-125.

Zachos, J., M. Pagani, L. Sloan, E. Thomas, and K. Billups. 2001. Trends, rhythms, and aberrations in global climate 65 ma to present. Science 292:686-693.

9. Conclusions

9. CONCLUSIONS

In this work the evolution of the genus *Megacricetodon* (Rodentia, Mammalia) during the Aragonian and Vallesian (middle and upper Miocene) have been studied. For this purpose 13.771 dental specimens of *Megacricetodon* from 75 localities of the Calatayud-Montalbán Basin and from 38 European localities have been studied, described and measured.

The morphological analyses were based in a matrix of 31 cheek teeth characters (M1, M2, M3, m1, m2, m3). This database was used to calculate the frequency of the character states in the different *Megacricetodon* assemblages. Besides, the nomenclature of the cheek teeth of *Megacricetodon* was updated to include all important characters used in the taxonomic work.

The results obtained from the analyses of the metrical and morphological patterns of the *Megacricetodon* associations from the Calatayud-Montalbán basin have been interpreted taxonomically. The comparison with *Megacricetodon* assemblages from other Miocene European basins allowed the proposition of a new paleobiogeographic framework.

Besides, the update in the *Megacricetodon* evolution has allowed us to refine the bioestratigraphy of the Aragonian and early Vallesian.

Three new species of *Megacricetodon* are proposed on this Thesis. In addition, other six taxa are described and studied. A revision of the previously proposed lineages is performed.

Megacricetodon vandermeuleni sp. nov. is a large-sized species from biozone Db (middle Aragonian) present in five localities in the Calatayud-Montalbán Basin and one locality in the Loranca Basin. The new species is biostratigraphicaly important because it is restricted to local zone Db. This new species coexisted with the small *Megacricetodon primitivus*, changing the proportion that represents each of the co-occurring species over time. In the older localities of the biozone, *M. vandermeuleni* is poorly represented, while, at the end of the local zone Db, it becomes the dominant *Megacricetodon* species in comparison to *M. primitivus*.

This species has close morphological similarities with the typical forms from central Europe. Based on these similarities, a European group of *Megacricetodon* species is proposed, the "*Megacricetodon bavaricus* group" which includes: *Megacricetodon* aff. *collongensis*, *M. bavaricus*, *M.* aff. *bavaricus*, *M. bezianensis*, *M. lappi*, *M. aunayi* and *M. vandermeuleni*. This group occurs in France, Switzerland and Germany during MN4, dispersing through Southwestern Europe during MN5.

The material of *Megacricetodon* from early to middle Aragonian (from local zone Ca to local zone Db) has been assigned to the small-sized *M. primitivus*. The species is recorded from 23 localities in the Calatayud-Montalbán Basin and one locality in the Loranca Basin. The observed evolutionary patterns of this specie are stable through time in size and dental morphology, although with high intra-populational variability.

The type collection of this species, Valtorres, have been restudied and described, proposing the correlation of this fauna to the local zone Da. The analyses carried out demonstrate that this material shows strong taphonomical deformations (fractures, compression, torsion…) that affect the metrical variability of this *Megacricetodon* assemblage.

The comparison with other European assemblages indicate that the geographical distribution of *Megacricetodon primitivus* is restricted to Southwestern Europe, specifically the Iberian Peninsula and France.

A new medium-sized species, *Megacricetodon alvarezae* sp. nov. is proposed. The species is present in eight middle Aragonian localities of the Calatayud-Montalbán Basin (uppermost part of local zone Db and local zone Dc).

Megacricetodon alvarezae sp. nov. is larger in size than *M. primitivus*. The new species maintains the dental morphology unchanged through time although exhibits a slightly decrease in size from oldest localities (Db and lowermost part of Dc) to the youngest ones.

Megacricetodon alvarezae sp. nov. is an endemic Iberian species, restricted to Portugal and Spain. The phylogenetic hypothesis proposed in the Thesis related this species with *M. primitivus*. The small *Megacricetodon primitivus* evolved towards morphologies similar to *Megacricetodon alvarezae* sp. nov. in Portugal and migrates into Spain at the end of the biozone Db (MN5). In the local zone Dc this species is the most common *Megacricetodon*.

The small-size *Megacricetodon collongensis* have been recognized in localities from the lower part of the local zone Dd, whereas the large-size *Megacricetodon gersii* have been recognized in localities from the upper part of local zone Dd and E. The study of the *Megacricetodon* material of 37 stratigraphically superposed localities from the Calatayud-Montalbán Basin allows us to propose that these *Megacricetodon* forms are two successive species within a single lineage. Moreover, the morphological similarities of the material included in *Megacricetodon collongensis* from the Calatayud-Montalbán Basin to *M. collongensis* from Vieux-Collonges, instead to *M. "collongensis"* from Port-la-Nouvelle support the existence of the lineage *M. collongensis - M. gersii*. The evolution from one species to the other is marked by changes in the dental morphology and by an increase in size. In the Calatayud-Montalbán Basin, these changes occurred approximately at the same time of one of the main sedimentological changes in the Basin.

In this Thesis, we assign to *Megacricetodon gersii* the *Megacricetodon* material from the middle Aragonian localities (local zone Dd and E) in the Calatayud-Montalbán Basin instead of that from the upper Aragonian (local zone F and G1) as previously thought. The bioestratigraphical and biochronological implications of this change is that *M. gersii* from the Iberian Peninsula predates its occurrence to Switzerland, changing the direction of the migration from Western Europe to Central Europe and also changing the magnitude of the diachrony (approximately 200ky instead of 400 ky).

In addition, we propose the "*Megacricetodon primitivus* group", a closely related group which includes *M. primitivus, M. alvarezae, M. collongensis* and *M. gersii*. These *Megacricetodon* forms are characterized by upper first molars having the anterocone deeply subdivided in most of the specimens, a lingual mesocingulum that connects the hypocone to the anterocone in more than 20% of the specimens. Lower first molars with similar height in the five main cusps and rounded anteroconid. This group occurred in France during the MN 4, dispersing through Spain and Portugal at the latest MN 4, and reaching Switzerland during MN 5.

Finally, a new large-sized species of *Megacricetodon*, *Megacricetodon bilbilis* sp. nov. is proposed after the study and revision of the material from the localities of the middle and upper Aragonian from the Calatayud-Montalbán Basin. This new species is distributed in the local zones E, F, and G1.

We propose this *Megacricetodon* form as part of the lineage *Megacricetodon bilbilis – M. crusafonti - M. crusafonti-ibericus – M. ibericus.* This lineage had its first occurrence in Spain with *M. bilbilis* sp. nov. during the upper part of local zone E, spreading during biozones F and G1, and evolving into *M. crusafonti* in local zone G2. The last occurrence of this lineage is in the local zone H (Vallesian) with the species *M. ibericus*. The trends shown by this lineage are towards a reduction of the mesolophs(ids) and a progressive subdivision of the anteroconid, but keeping constant its dimensions.

The geographical distribution of the lineage *Megacricetodon bilbilis – M. ibericus* is restricted to the Iberian Peninsula and possibly to France.

The species *Megacricetodon gersii* has been excluded of this lineage, based on important morphological and metrical differences found between them, and also based on the co-occurrence of *M. gersii* and *M. bilbilis* sp. nov. in several localities in the Calatayud-Montalbán Basin.

We proposed that the entrance of *Megacricetodon* in Europe is not a single bioevent, but at least three migration waves:

The first event that we recognize is the migration of the Greek *Megacricetodon*. These small-sized forms were endemic of the Greek area and are recorded from the earliest MN 4.

The second migration wave is the *Megacricetodon bavaricus* group. These large-sized forms of *Megacricetodon* were mainly distributed in the Central-European basins. This group will not reach the Iberian Peninsula till middle MN 5.

The third event was the migration of the *Megacricetodon primitivus* group. These Southwestern *Megacricetodon* forms occurred in France in the lower Aragonian, and reached Central Europe (Switzerland) in the middle Aragonian.

Finally, we recognize the *Megacricetodon bilbilis – M. ibericus* lineage. These large-sized forms are endemic of the Southwestern Europe, first recorded in Spain in middle Aragonian.

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